DOCTORAL THESIS

Carbon stock and fluxes in Nyungwe forest and Ruhande Arboretum in Rwanda

Donat Nsabimana

DEPARTMENT OF PLANT AND ENVIRONMENTAL SCIENCES
FACULTY OF SCIENCE
UNIVERSITY OF GOTHENBURG

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Examiner: Prof. Åke Larsson, University of Gothenburg, Sweden
Faculty Opponent: Prof. Daniel Epron, Université Henri Poincaré Nancy 1, France

E-mail addresses: donat.nsabimana@dpes.gu.se, dnsabimana@nur.ac.rw

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ABSTRACT

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Conservation and sequestration of carbon in forest ecosystems are potential strategies to reduce or stabilize the atmospheric greenhouse gas concentrations and mitigate climate change. Estimating the degree to which forest ecosystems may achieve that function requires continuous measurements of forest carbon stocks and fluxes from all over the world. The aim of this thesis was to collect quantitative data on climate, carbon stocks, annual carbon increment, litter production, and soil CO_2 effluxes in Ruhande Arboretum, a plantation of both non-native and native tree species, and Nyungwe forest, a national park of afromontane tropical forest vegetation, both situated in Rwanda. The annual mean air temperature at the Ruhande Arboretum (19 ºC) was higher than in the Nyungwe forest (14.4 ºC), but both sites showed small seasonal variation in air temperature and Nyungwe forest received a higher monthly precipitation than the Ruhande Arboretum. The carbon stocks were dominated by above-ground biomass in both forests which was 70% in the Ruhande Arboretum and 57% in the Nyungwe forest. The annual litter production was 3.4 Mg C ha^{-1} yr^{-1}, and followed a seasonal pattern. The mean annual soil CO_2 efflux was 13.5 Mg C ha^{-1} yr^{-1} in the Ruhande Arboretum and 10.2 Mg C ha^{-1} yr^{-1} in the Nyungwe forest. No significant effect by the species on soil CO_2 efflux was observed. The seasonal variation in soil CO_2 efflux was strongly influenced by precipitation patterns and soil water content. Diurnal variation of soil CO_2 efflux was bimodal and described a hysteresis relationship with soil temperature. Although, the daytime soil CO_2 efflux correlated with soil temperature, the most of diurnal pattern was most likely affected by the supply of photosynthetic products to the roots. Spatial variation of soil CO_2 efflux was mainly correlated to soil C and N stocks. The observed spatial, seasonal and annual soil CO_2 effluxes were comparable to those observed in other tropical forests. This study should be replicated in other forests and in other land cover types in Rwanda, which can help to calculate a carbon balance for Rwanda.

Keywords: Carbon stock; Litterfall production; Soil CO_2 efflux or soil respiration; Soil temperature; Soil water content; Spatial variation; Seasonal and diurnal variations.

LIST OF PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I. Nsabimana D., Klemedtsson L., Kaplin B.A., Wallin G., 2008. Soil carbon and nutrient accumulation under forest plantations in Southern Rwanda. African Journal of Environmental Science and Technology 2 (6), 142–149.

II. Nsabimana D., Klemedtsson L., Kaplin B.A., Wallin G., 2009. Soil CO_2 flux in six monospecific forest plantations in southern Rwanda. Soil Biology and Biochemistry 41, 396–402.

III. Nsabimana D., Klemedtsson L., Wallin G. Seasonal and diurnal variation of soil respiration in monospecific stands of *Entandrophragma excelsum* and *Eucalyptus maculata* in Rwanda. *In manuscript*.

IV. Nsabimana D. and Wallin G. Spatial and temporal variations of soil CO_2 efflux in Nyungwe mountain tropical forest in Rwanda. *In manuscript.*.

V. Nsabimana D. and Wallin G. Carbon stock, annual carbon increment and litterfall production in Ruhande Arboretum and Nyungwe forest in Rwanda. *In manuscript*.

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1. INTRODUCTION

Forest ecosystems occupy large landscape areas of our planet and they play important socio-economic roles for human populations, and they also provide valuable ecological and environmental services. Thus, continuous monitoring of patterns of forest ecosystem functioning is needed for better understanding of global environmental change and to allow predictions of future human well-being.

1.1 The world's forest

Forest ecosystems supply to human populations products such as fuelwood, charcoal, construction materials and other valuable products (UNEP, 2002; Montagnini and Jordan, 2005; **Paper I**). Forest cover helps to maintain a thermal balance in the atmosphere through evapotranspiration; forests regulate hydrological cycles, soil and water quality, and support the highest biodiversity (UNEP, 2002; Montagnini and Jordan, 2005; Denman et al., 2007; Bonan, 2008). They play a major role in carbon storage and exchange with the atmosphere and regulation of climate (Dixon et al., 1994; Field et al., 1998; FAO, 2001; Denman et al., 2007; Bonan, 2008).

The world's forested area was recently estimated at 3 952 million hectares (Mha), accounting for 25.3% in Europe, 21% in South America, 17.9% in North America, 16% in Africa, 14.5% in Asia, and 5.2% in Oceania (FAO, 2006). In the tropics, forests were estimated to cover an area of 2675 Mha in 1850 (Malhi et al., 1999), 1910 Mha in 1980 and 1756 Mha in 1990 (FAO, 2001). South America has the largest tropical forest area (886 Mha), followed by the Congo Basin and the Indonesian Archipelago (FAO, 2001; Chao et al., 2009). Two-thirds of the world's forest is distributed in ten countries, with largest forest areas in the Russian Federation (809 Mha), Brazil (478 Mha), Canada (310 Mha), United States (303 Mha) and China (197 Mha) (FAO, 2006).

1.2 Rwandan forests

Information on Rwandan forests (Fig. 1b) is mainly limited to its geographical distribution, plant species composition, and historical land use changes (FAO, 1993, 2000). The Rwandan forests are composed of natural forests, woodlands, savannas and forest plantations, and were historically heavily deforested as a result of increased demand for agricultural land, grazing land, settlement and urbanization sites, and fuelwood (FAO, 2000; UNEP, 2002; MINITERE, 2003). The total area forested in Rwanda was 30% of total land area in the 1930s (Masozera and Alavalapati, 2004), 25.7% in 1960 and has been reduced to 8.9% in 2000

(MINITERE, 2005). In 2005, the MINITERE and CGIS-NUR forest mapping project estimated the Rwandan forest cover to be 240 746 ha, equivalent to 10.1% of national land area and subdivided into humid natural forests (3.4%), degraded natural forests (1.6%), bamboos and savannah (0.34%) and forest plantations (4.8%) (Fig. 1b; MINITERE and CGIS-NUR, 2007). The area of natural forest has decreased over time since 1960 while forest plantations has increased from 1960 to 2005, mainly composed of introduced tree species including the genera of *Eucalyptus*, *Grevillea, Cedrella, Pinus, Cupressus* and *Callitris,* of which *Eucalyptus* occupied 65% of the total plantation area (FAO, 2000; **Paper I**). With reference to the literature (e.g., MINITERE, 2003; FAO, 2000), it became evident that there was a lack of field data characterizing the status of biomass, carbon stock and fluxes, and soil nutrient content in Rwandan forests; thus it is a high need for further research.

1.3 Global carbon cycle in forest ecosystems

When nations convened and signed the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto protocol, forest preservation, reforestation, and afforestation practices were proposed as options to conserve and enhance carbon sequestration, and potentially reduce or stabilize atmospheric greenhouse gas concentrations and mitigate climate change (Dixon et al., 1994; IPCC, 2000; Montagnini and Jordan, 2005; Houghton, 2007; Luyssaert et al., 2007; Bonan, 2008). Research activities on the role of forests in the carbon cycle have also emerged, aiming to increase the understanding of the main processes in the carbon cycle.

The major carbon reservoirs are estimated to be oceans (38000 Pg C), terrestrial vegetation (500 Pg C), soils (1500–2000 Pg C), fossil fuels (5000–10 000 Pg C) and atmosphere (780 Pg C) (IPCC, 2000; Janzen, 2004; Houghton, 2007; Lambers et al., 2008). The exchanges of carbon between the atmosphere and terrestrial ecosystems (soil and vegetation) is critical to the patterns of carbon dioxide concentration in the atmosphere (Luo and Zhou, 2006; Houghton, 2007; IPCC, 2007; Lambers et al., 2008).

The amount of carbon dioxide (CO_2) – the main anthropogenic greenhouse gas in the atmosphere– has significantly increased since the beginning of industrial revolution from about 275–285 ppmv (parts per million by volume) to over 385 ppmv in 2008, and continues to rise by 1.5 ppmv per year, and contributes 63% of the radiative forcing of climate change caused by the main greenhouse gases (IPCC, 2000; Houghton, 2007; IPCC, 2007; Lambers et al., 2008). Carbon is returned to the atmosphere via three of the largest fluxes, oceanic release (~90 Pg C yr^{-1}), plant respiration (~59 Pg C yr^{-1}), and soil respiration (~58 Pg C yr^{-1}) (Schlesinger, 1997; IPCC, 2000; Luo and Zhou, 2006; Houghton, 2007; Lambers et al., 2008). These fluxes are mainly countered by plant photosynthesis which absorbs ~120 Pg C yr^{-1} from the atmosphere and ocean uptake (~92 Pg C yr^{-1}). In addition, there are two small but fluxes where CO_2 is released from land use changes (~2 Pg C yr^{-1}) and taken up by vegetation increases elsewhere (~0.7 Pg C yr^{-1}). This means that carbon accumulated in vegetation (500 Pg C), detritus and soils (1500–2000 Pg C) (Malhi et al., 1999; Luo and Zhou, 2006) are decreasing of a rate of ~1.3 Pg C yr^{-1}. It is accepted that the most recent increases in atmospheric CO_2 concentration are mainly caused by human activities, namely the combustion of fossil fuels, cement production, land use changes and biomass burning; they emit to the atmosphere 8 Pg C yr^{-1} (Janzen, 2004; Luo and Zhou, 2006; IPCC, 2007; Lambers et al., 2008), which exceeds the net ocean and land sinks (3.1 Pg C yr^{-1}; IPCC, 2007). This has altered the natural carbon cycle and contributed significantly to climate change (Houghton, 1999; Malhi et al., 1999; Houghton, 2007; IPCC, 2007).

The flux of carbon returned to the atmosphere through soil respiration, has received considerable research attention because it remains the least understood among the processes of the global carbon cycle (Luo and Zhou, 2006); it originates from the respiration of plant roots, soil microorganisms and soil macrofauna, as well as a small fraction of CO_2 that comes from chemical oxidation and carbonate dissolution (Raich and Schlesinger, 1992; Valentini, 2003; Epron et al., 2004a; Sotta et al., 2004; Lee et al., 2006; **Paper II**). Soil respiration in forests utilizes more than 50% of carbon assimilated in gross ecosystem photosynthesis (Gaumont-Guay et al., 2006; Luo and Zhou, 2006) and contributes to 30–80% of total ecosystem respiration (Luo and Zhou, 2006). Soil CO_2 efflux from tropical forests was estimated to be an average of 12 Mg C ha^{-1} yr^{-1} and between 3.2–6.8 Mg C ha^{-1} yr^{-1} in temperate and boreal forests (Raich and Schlesinger, 1992; Luo and Zhou, 2006).

Soil respiration will probably continue to receive more research priority because previous soil respiration studies were not equally distributed in different geographical regions and some regions remain unstudied. Consequently, estimates of global soil CO_2 effluxes are still associated with large uncertainties which cause difficulties in predicting future soil CO_2 efflux with precision (Houghton, 1999).

On the other hand, forest ecosystems have received more research interest because of their significant role in the global carbon cycle and global atmospheric change (Houghton, 1999; Malhi et al., 1999; IPCC, 2001; IPCC, 2007). Forests are the largest carbon stock in terrestrial ecosystems (IPCC, 2000; Geider et al., 2001; Janzen, 2004; Roxburgh et al., 2006; Bonan, 2008) estimated to be about 1150 Gg (Dixon et al., 1994), of which 49% is in boreal forests, 37% in tropical forests and 14% in temperate forests (Malhi et al., 1999).

Forest ecosystems make the largest contribution to global primary production (Malhi et al., 1999). For instance, net primary productivity (NPP) of tropical forests is estimated at 8 Mg of C ha^{-1} yr^{-1} (Schlesinger, 1997; Field et al., 1998), and between 3.1–31.5 Mg C ha^{-1} yr^{-1} (Clark et al., 2001) and contribute 32–36% of terrestrial NPP (Clark, 2004; Adachi et al., 2006; Bonan, 2008). A large fraction of living biomass is returned to soils as dead organic matter, including litterfall, root detritus and root exudates, which consequently increase the amount of carbon stored in the soil profiles (Schlesinger, 1977; Brown and Lugo, 1982; Clark et al., 2001). For instance, the Amazon forest is one of the most substantial biomass carbon pools and stores about 9.6 Pg C in dead wood, which range between 2.5−86.6 Mg ha^{-1} (Chao et al., 2009).

In the past two decades, the importance of forests in the global carbon cycle and global atmospheric changes has led to increased research attention focused on whether forest ecosystems will continue to absorb carbon or will become a source of carbon dioxide to the atmosphere (Malhi et al, 1999; Mo et al., 2005), and therefore document or support the proposal that reforestation and afforestation activities will stabilize the atmospheric carbon dioxide concentration and mitigate climate change (IPCC, 2000; Montagnini and Jordan, 2005; Luyssaert et al., 2007). Most information on the role of forests in the carbon stock and flux processes between plants, soil and atmosphere generally comes from boreal and temperate regions, and tropical America, but less attention has been given to Africa (Cao et al., 2001; **Paper II**). Because of the small number of such studies in tropical Africa, this could produce large errors in estimates of the global carbon balance (Houghton, 2005).

The tropical African climate is different from that of tropical America and Asia, which is characterized by lower precipitation, higher soil water stress and cooler air temperature because tropical Africa is to a larger extent situated at higher altitudes (McGregor and Nieuwolt, 1998; Malhi and Wright, 2004). These facts suggest the need to compare carbon storage and cycling patterns in tropical Africa to those in other regions. The African continent has also been warming at the rate of about 0.5 ºC per century during the 20th century, with larger warming in the June−August season, and it is predicted that Africa will be between 2−6 ºC warmer in 100 years (Hulme et al., 2005), indicating a need to predict the warming impact on carbon storage and fluxes in African forests.

2. AIMS

Predicting the future carbon balance in Rwandan forest ecosystems requires an estimation of forest carbon pools and fluxes. It is needed to estimate soil CO_2 release which is a key element of ecosystem respiration, and determine the factors that control its variation, including soil temperature and soil water content, which control global soil CO_2 emission (Raich and Schlesinger, 1992; Raich et al., 2002; Gaumont-Guay et al., 2006; Luo and Zhou, 2006).

Field data on carbon pools and fluxes are also needed for the estimation of sources and sinks of greenhouse gases at the national level to be reported to the UNFCCC, which Rwanda has ratified, to predict the carbon-sequestration potential of Rwandan land, and to support political decisions in relation to climate change mitigation strategies. At regional scale, studies of carbon stocks and fluxes in Rwandan forests will contribute to refined calculations of global carbon balance and help identify missing carbon sinks.

The aim of this thesis was to collect quantitative data on climate, carbon stocks, annual carbon increment, litter production, and soil CO_2 effluxes in a forest plantation and a native forest in Rwanda. More specific aims of the five papers were to:

I. Estimate carbon stocks in soil, litter, aboveground biomass and belowground biomass in the Ruhande monospecific forest plantations and Nyungwe mountain tropical forest (**Papers I**, **II**, **IV** and **V**).
II. Estimate the aboveground biomass increment and determine the seasonal pattern of litter production in monospecific plantations (**Paper V**).
III. Document quantitative data on diurnal, seasonal and spatial variations in soil CO_2 efflux in the Ruhande monospecific forest plantations and the Nyungwe forest (**Papers II**, **III**, and **IV**);
IV. Determine the dominant factors creating the variations in soil CO_2 efflux, particularly the responses of soil, stand, and climate characteristics (**Papers II**, **III**, and **IV**).

Forest land uses were selected for the studies because they store the largest amount of carbon in soils and biomass and are potentially the largest CO_2 sources. The Nyungwe forest and the Ruhande Arboretum were also selected for the studies because their long-term land use history was known and they represent both native forest and forest plantation types, respectively.

3. MATERIALS AND METHODS

3.1 Sites description

The studies were carried out in two forest types that were situated at two geographical locations (Fig. 1): (i) the Ruhande Arboretum covers 200 ha divided into 504 plots of monospecific stands and 4 ha of mixed native species (MNS), situated in southern Rwanda (2º36′S, 29º44′E, 1638–1737 m altitude); and (ii) the Nyungwe montane tropical forest, covers an area of 970 km^2 of mountain forest situated in southwestern Rwanda (2°17′–2°50′S, 29°07′–29°26′E, 1600–2950 m altitude). Nyungwe forest is also a national park. The number of sites varied through the study: three replicates of seventeen monospecific stands and a MNS plot (**Paper I**), two replicates of six monospecific stands (**Paper II**), two replicates of two monospecific stands (**Paper III**), four plots in the Nyungwe forest (**Paper IV**), and three replicates of eight monospecific forest plantations, three replicates in the MNS plot, and four plots in the Nyungwe forest (**Paper V**). The sites were characterized in **Papers I** to **V** in relation to tree species composition, tree density, stand age, diameter at breast height (DBH), height, basal area, and leaf area index (LAI).

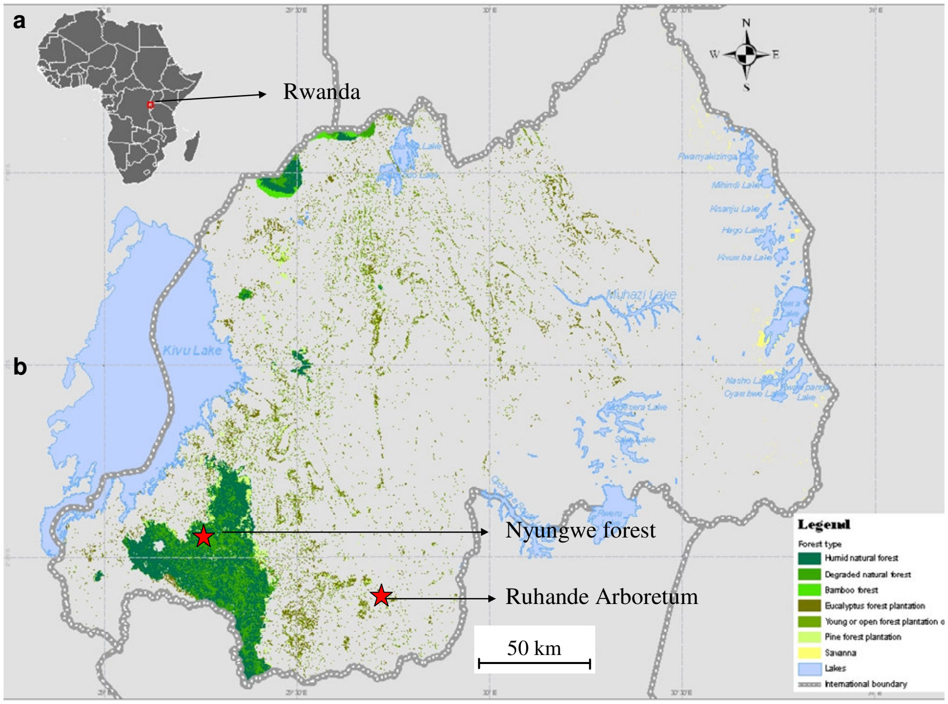

Figure 1. Location of Rwanda in Africa (a). Map of Rwandan forests showing the two research sites: the Nyungwe forest and Ruhande Arboretum and location of weather stations in red stars (b) (**Papers I–V**).

3.2 Meteorological measurements

The climate of the sites was monitored using two automated weather stations (Fig. 1b), which are described in details in **Papers III** and **IV**. One climate station was established in February 2006 in Butare city (2º35′ S, 29º44′E, 1765 m altitude) at about 2 km from the Ruhande Arboretum; Another climate station was established in February 2007 at Uwinka research site (2°28′43"S, 29°12′E, 2465 m altitude) in Nyungwe forest.

3.3 Soil sampling and analyses

Soil samples were taken from 0 to 10 cm, 10 to 20 cm, and 20 to 30 cm depths (**Papers II**, **IV**, and **V**) within each plot using stainless steal metallic cylinders of 7 cm diameter and 10 cm depth, and oven-dried at 105 ºC until constant weight for bulk density determination, and prepared for C and N concentrations analyses as outlined in **Papers II**, **IV**, and **V**. Soil samples were also analyzed for pH and nutrient contents as described in **Paper I**. Soil C concentrations were converted to soil C stocks (Mg ha^{-1}) following the method by IPCC (equation 3.2.16 in IPCC, 2003):

$$\text{SCD} = [\text{SOC}] * \text{Bulk Density} * (1 - \text{frag}) * \text{Depth} * 10$$

where *SCD* is a soil carbon density (t C ha^{-1}); *[SOC]* is the concentration of soil organic carbon in g C (kg soil)$^{-1}$; *Bulk Density* is a measure of soil bulk density (t m^{-3}); *frag* is % volume of coarse fraction (dimensionless); and *Depth* is the thickness of the soil layer sampled (m).

3.4 Estimation of current carbon storage

The carbon stocks were measured in soil, litter, and living biomass components (**Papers II**, **IV**, and **V**). The carbon stock in soil was determined as outlined in section 3.3. The procedure for the calculation of carbon stocks in litter and living biomass (**Paper V**) involved the determination of the dry mass of each component per hectare and the determination of its carbon concentration by dry combustion using an elemental analyzer, model EA 1108 CHNS. The carbon stock (Mg ha^{-1}) of each component was obtained by multiplying the carbon concentration by its dry mass per hectare. The detailed methodology is described in **Paper V**.

3.5 Estimation of vegetation biomass and mean annual increment

Current tree measurements of DBH and height (**Paper V**) were made in August 2008 and were complemented by historical measurements made by the managers of the Ruhande Arboretum. The DBH and height of trees in Nyungwe forest were measured in July 2008. For all trees within the plots having a stem DBH greater than 10 cm, DBH and height were measured, and these were used to calculate the aboveground volume using the allometric equation (FAO, 2004, p. 19). The wood density was determined using the method by Standards Australia (2000) in which samples were collected from the field and oven-dried at 70 ºC for 48 hrs. The total biomass (Mg ha^{-1}) was calculated by multiplying the volume over bark, wood density and biomass expansion factor (FAO, 1997, 2001). The annual biomass increment was determined by dividing total biomass with the age of the plantation. The obtained value was multiplied by the carbon concentration of dry wood sample to obtain the carbon increment per hectare and per year (**Paper V**).

3.6 Estimation of litterfall production

Litterfall was collected biweekly from May 2008 to October 2009 (**Paper V**) in three replicates of eight monospecific plantations in the Ruhande Arboretum. The litter was oven-dried at 70 ºC for 48 hrs and weighed for each date and averaged for each month. Litter samples collected in February and March 2009 were used to determine the carbon concentration in litterfall. Oven-dry litter samples were ground to a fine powder using a ball mill (model MM 301, Retsch, Germany) and their carbon concentrations were determined by dry combustion using an elemental analyzer, model EA 1108 CHNS. The dry mass of litterfall per hectare and per month was multiplied by litter carbon concentration. The monthly values obtained from June 2008 to May 2009 were summed to obtain the annual carbon accumulation by the litterfall. The detailed methodology for the litterfall measurement is given in **Paper V**.

3.7 Spatial and seasonal soil CO_2 efflux measurements

Spatial and seasonal variations of soil CO_2 efflux (µmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) were measured in two replicates of six monospecific forest plantations at the Ruhande Arboretum (**Paper II**) and in four plots in the Nyungwe forest (**Paper IV**) using the LI 6400–09 soil respiration chamber connected to the LI–6400 Portable Photosynthesis System (LI–COR Inc., Lincoln, NE, USA) (Fig. 2a). Simultaneously, soil temperature at 10 cm depth was monitored using a soil probe thermocouple (LI 6000–09 TC, LI–COR Inc., Lincoln, NE, USA) connected to a data logger and inserted in the soil adjacent to the soil respiration chamber. Soil water content was measured at the 3 points closest to the measurement positions using a Theta probe (Ml2, Delta-T Devices Ltd., Cambridge, U.K.) inserted at 6 cm soil depth. The detailed procedure for these measurements is given in **Papers II** and **IV**.

3.8 Diurnal soil CO_2 efflux measurements

The diurnal soil CO_2 effluxes were measured in two plots of *Eucalyptus maculata* and two plots of *Entandrophragma excelsum* at the Ruhande Arboretum (**Paper III**) and in Yellow trail plot in Nyungwe forest (**Paper IV**). Diurnal patterns of soil CO_2 efflux (µmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$) were measured once a month for 48 consecutive hours at 10 minutes intervals, using the LI–8100 automated soil CO_2 flux system connected to the LI–8100-101 soil chamber (LI–COR Inc., Linkoln, NE, USA) (Fig. 2b). Simultaneously, soil temperature (°C) and soil water content were recorded using accessory sensors (LI–8100-201 soil temperature probe and an EC-5 dielectric sensor for soil water content, respectively) that were attached to the LI–8100 automated soil CO_2 flux system and inserted in the soil to a depth of 10 cm, close to the LI–8100-101 soil chamber (**Papers III** and **IV**). Alternatively, soil temperature and soil water content were monitored every 10 minutes using soil temperature sensors and soil moisture sensors, Theta Probes (Delta-T Devices Ltd., Cambridge, U.K.) that were attached to a GP1 data logger (Delta-T Devices Ltd., Cambridge, U.K.). The detailed protocol is described in **Papers III** and **IV**.

3.9 Data analyses

Measurements of soil CO_2 efflux, soil temperature, and soil water content from sampling locations at each site were averaged to give a monthly mean for each site. The monthly mean soil CO_2 effluxes were averaged to give an annual efflux (μmol m^{-2} s^{-1}) (**Papers II**, **IV**). The rate of soil CO_2 efflux in **Papers II** and **IV** (μmol m^{-2} s^{-1}) was converted to Mg C ha^{-1} yr^{-1} (1 Mg = 10^6 g), expressing the annual carbon emission per hectare, as following:

$$1\ \mu mol\ CO_2\ m^{-2}\ s^{-1} = 0.086\ mol\ CO_2\ m^{-2}\ d^{-1} \approx 1.04\ g\ C\ m^{-2}\ d^{-1} = 3.78\ Mg\ C\ ha^{-1}\ yr^{-1}$$

The diurnal patterns of soil CO_2 efflux was analysed by identifying the time of the minimum (t_{Min}) and maximum (t_{Max}) and the amplitude of the variation (**Paper III**). Soil CO_2 efflux was averaged for three periods of day: 06:00–10:00 hrs, 10:00–14:00 hrs and 14:00–18:00 hrs and identified the minimum and maximum soil CO_2 efflux (SCE_{Min} and SCE_{Max}) at each t_{Min} and t_{Max} point and calculating the diurnal amplitude of soil CO_2 efflux (**Paper III**).

One-way analysis of variance (ANOVA) with the Tukey's *post hoc* test at $\alpha = 0.05$ was used to compare treatments in relation to carbon stock in soil, litter, and biomass and soil nutrient contents (**Papers I**, **II**, **IV** and **V**). Repeated measures analysis of variance (RMANOVA) at $\alpha = 0.05$ was used to test for differences in temporal variation of soil CO_2 efflux, soil water content and soil temperature (**Papers II**, **III** and **IV**). Pearson correlation analysis was used to examine the relationship between soil CO_2 effluxes and soil and stand variables (**Papers II** and **IV**). Standard deviation (SD) and coefficient of variation (CV) were used to express the temporal and spatial variability of soil CO_2 effluxes. Statistical analyses were performed using SPSS software, version 15.

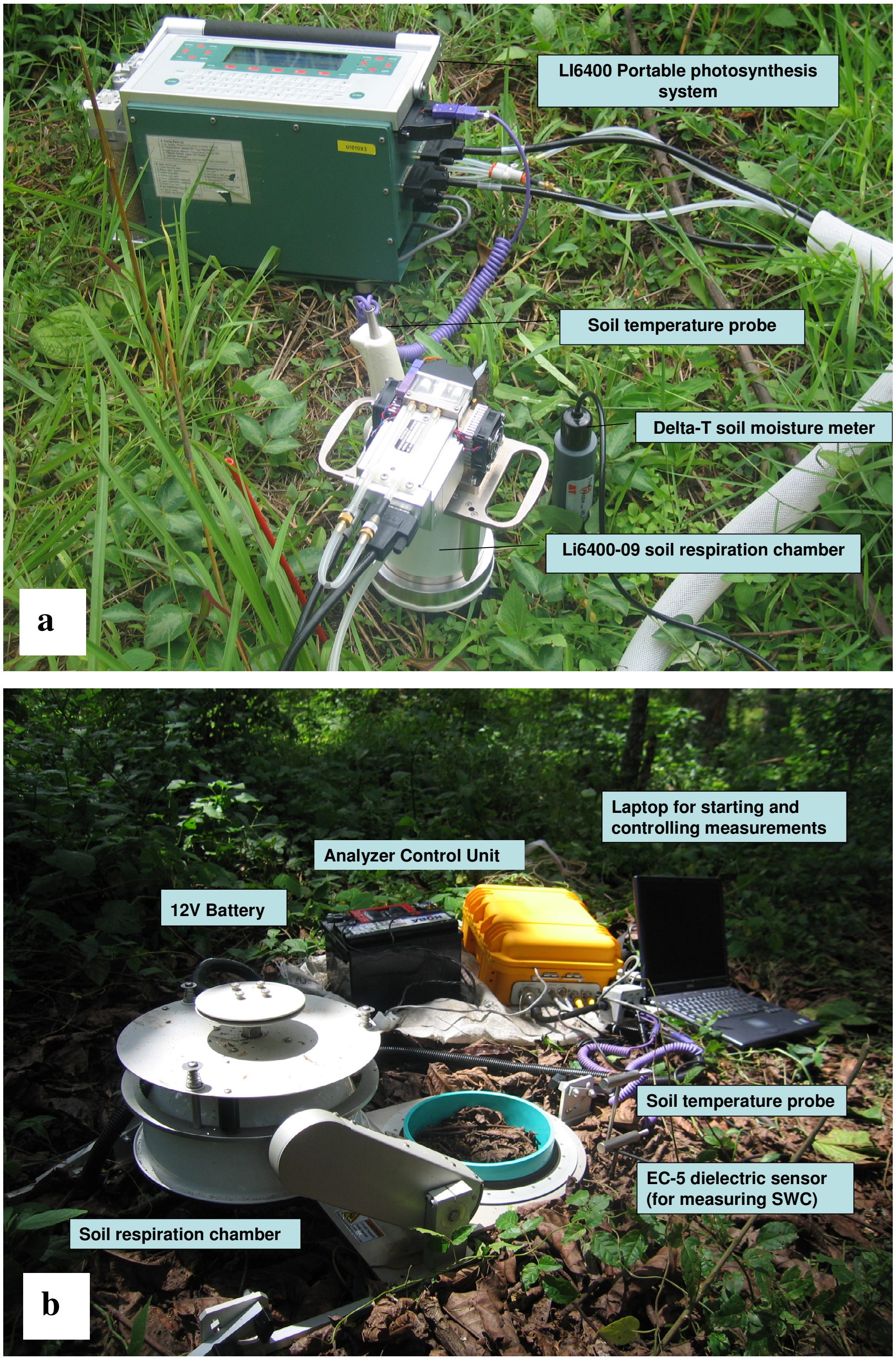

Figure 2. Measurement of soil CO_2 efflux in the field using the LI−6400 soil respiration system (a) and Diurnal soil CO_2 efflux measurement using the LI−8100 automated soil CO_2 flux system (b) (**Papers II**, **III**, and **IV**).

4. RESULTS AND DISCUSSION

4.1 Climate

The Nyungwe forest and Ruhande Arboretum are characterized by a climate with a bimodal rainfall pattern: two rainy seasons alternating with two dry seasons (**Papers II**, **III**, and **IV**). The main rainy season extends from March to May and the mild rain extends from September to December. In 2007 and 2008, the Nyungwe forest received a higher monthly precipitation than the Ruhande Arboretum (Figs. 3c, d), while annual mean air temperature at Ruhande was higher (19 ± 0.5 ºC; Fig. 3a) than that in the Nyungwe forest (14.4 ± 0.5 ºC; Fig. 3b), but both sites showed small seasonal variations in air temperature (Fig. 3a, b; **Papers II**, **III** and **IV**).

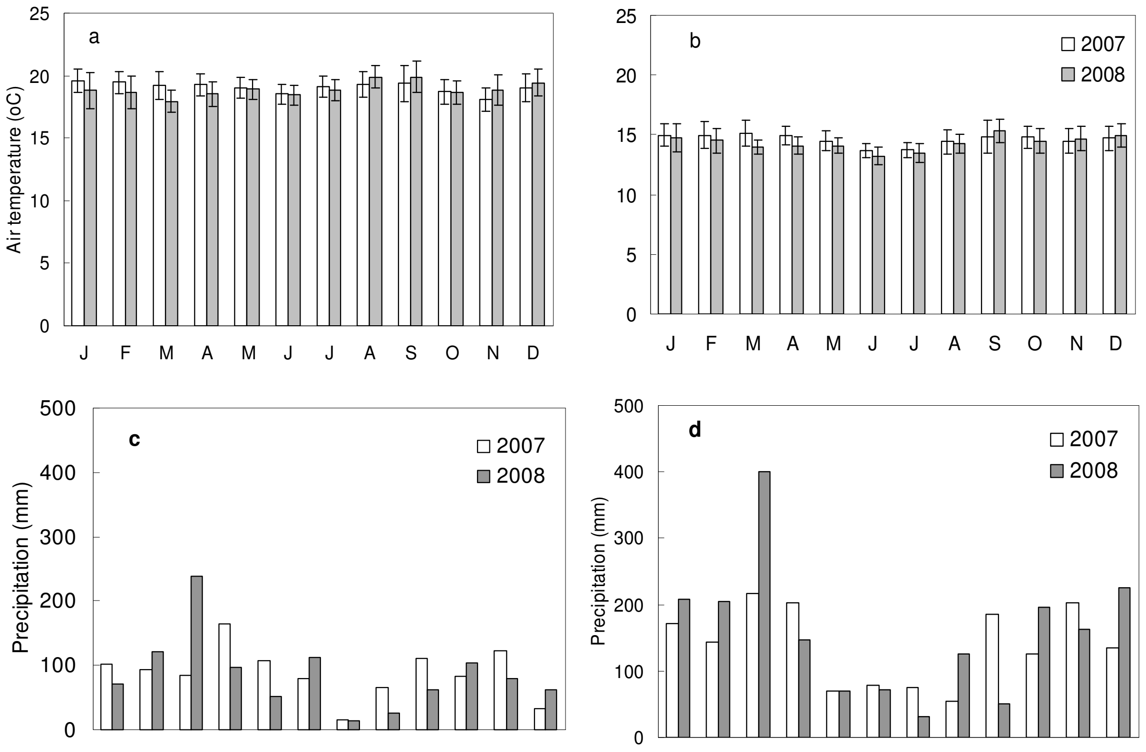

Figure 3. Monthly mean air temperature in the Ruhande Arboretum (a) and Nyungwe forest (b) and monthly precipitation in Ruhande Arboretum (c) and Nyungwe forest (d) in 2007 and 2008 (**Papers II**, **III**, and **IV**). Error bars in (a) and (b) indicate standard deviation from the monthly mean air temperature. Annual mean air temperature in Ruhande Arboretum was 19 ± 0.5 ºC ranging between 17.9 ± 0.9 ºC in March 2008 and 19.9 ± 1.3 ºC in September 2008. Annual mean air temperature in the Nyungwe forest was 14.4 ± 0.5 ºC ranging between 13.2 ± 0.76 ºC in June 2008 and 15.3 ± 0.97 ºC in September 2008. The main dry season occurs in July and August.

4.2 Carbon storage in different pools

The carbon stock (**Paper V**) in the Ruhande monospecific plantations (711 ± 387 Mg C ha^{-1}) was higher than that in the Nyungwe forest (659 ± 177 Mg C ha^{-1}), but not significantly different (Fig. 4; P = 0.66), and were higher than the values observed in other tropical forests (**Paper V**), but soil carbon and litter carbon stocks were higher in Nyungwe forest than in the Ruhande Arboretum (Fig. 4; P < 0.001). The largest fraction of total carbon stock was in aboveground biomass, accounting for 70% in the Ruhande Arboretum and 57.3% in the Nyungwe forest (**Paper V**).

The spatial distributions of carbon pools in the Ruhande Arboretum were more variable than those in Nyungwe forest (Table 1; Data from **Paper V**), which may have resulted from differences in species productivity, the removal of biomass when trees were harvested or thinned, and the collection of firewood by the neighboring population at the Ruhande Arboretum. The relative stability of carbon pools in the Nyungwe forest may be explained by its long-term accumulation of litterfall and coarse wood debris and its status as a protected area by the Rwandan Government. Moreover, litter decomposition and microbial activity are faster at higher temperatures (Raich et al., 2006), suggesting a slower decomposition rate in the Nyungwe forest than in the Ruhande Arboretum because the climate in the Nyungwe forest was 4.6 ºC cooler than that in the Ruhande Arboretum (Fig. 3). Thus the balance between mortality inputs and decomposition outputs become relatively higher in the Nyungwe forest.

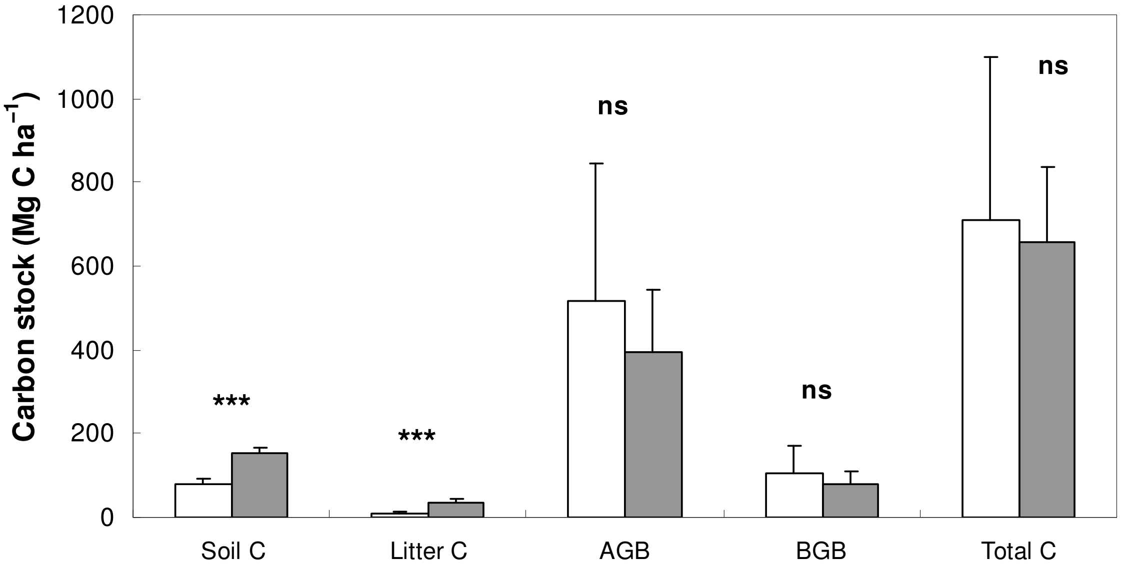

Figure 4. Estimates of carbon stock (Mg C ha^{-1}) in soil, litter, aboveground biomass (AGB), belowground biomass (BGB), and total carbon stock (Total C) in the Ruhande Arboretum (white bars) and the Nyungwe forest (grey bars). Vertical bars indicate standard deviation from the mean. Statistical analysis (t-test): *** P < 0.001; ns: not significant (**Paper V**).

Table 1. Comparison of spatial distribution of carbon pools in the Ruhande Arboretum and the Nyungwe forest, expressed using coefficient of variation (%). Abbreviations: aboveground biomass (AGB), belowground biomass (BGB), soil carbon (Soil C), litter carbon (Litter C), and total carbon (Total C) (Data from **Paper V**).

Site name	Soil C	Litter C	AGB	BGB	Total C
Ruhande	15.1	47.7	63.1	54.4	54.5
Nyungwe	7.9	23.8	38.1	38	26.9

4.3 Aboveground biomass increment and litterfall production

The annual aboveground carbon increment (**Paper V**) was between 3.3 and 14.7 Mg C ha^{-1} yr^{-1} and was largest in *Eucalyptus microcorys* and *Eucalyptus citriodora* stands and lowest in *Afrocarpus falcatus* stands at the Ruhande Arboretum. Annual litter production (**Paper V**) was 3.4 Mg C ha^{-1} yr^{-1}, ranging between 2.3 and 4.2 Mg C ha^{-1} yr^{-1} and was largest in *Polyscias fulva* and *Entandrophragma excelsum* stands, both are native forest species (Table 4 in **Paper V**). Litter production followed a seasonal pattern with lowest values during wet seasons and highest values in dry seasons (Fig. 2 in **Paper V**). The litter production rate was comparable to the values observed in other tropical forests, while the biomass increment in our study site was larger than the values from other tropical forests (**Paper V**).

4.4 Mean annual and spatial variations of soil CO_2 efflux

The mean annual soil CO_2 efflux in the Ruhande monospecific plantations (13.5 Mg C ha^{-1} yr^{-1}; **Paper II**) was higher than that in the Nyungwe forest (10.2 Mg C ha^{-1} yr^{-1}; **Paper IV**). In the Ruhande Arboretum, mean annual soil CO_2 efflux was highest in *E. saligna* stand (14.7 Mg C ha^{-1} yr^{-1}) followed by the *E. maidenii* stand (14.3 Mg C ha^{-1} yr^{-1}) and the *E. maculata* stand (13.4 Mg C ha^{-1} yr^{-1}) and lowest in *Entandrophragma excelsum* stand (11.7 Mg C ha^{-1} yr^{-1}), but with no significant difference between species (Fig. 5a; **Paper II**). In Nyungwe forest, mean annual soil CO_2 efflux was highest in YTP and BTP (11.7 and 11.1 Mg C ha^{-1} yr^{-1}, respectively; Fig. 5b). Soil CO_2 efflux rates in our studies were in the range of previous results in other tropical regions (Table 2; 7–26 Mg C ha^{-1} yr^{-1}: Raich and Schlesinger, 1992; Buchmann et al., 1997; Davidson et al., 2000; Schwendenmann et al., 2003; Epron et al., 2004b; Salimon et al., 2004; Sotta et al., 2004; Epron et al., 2006a, b).

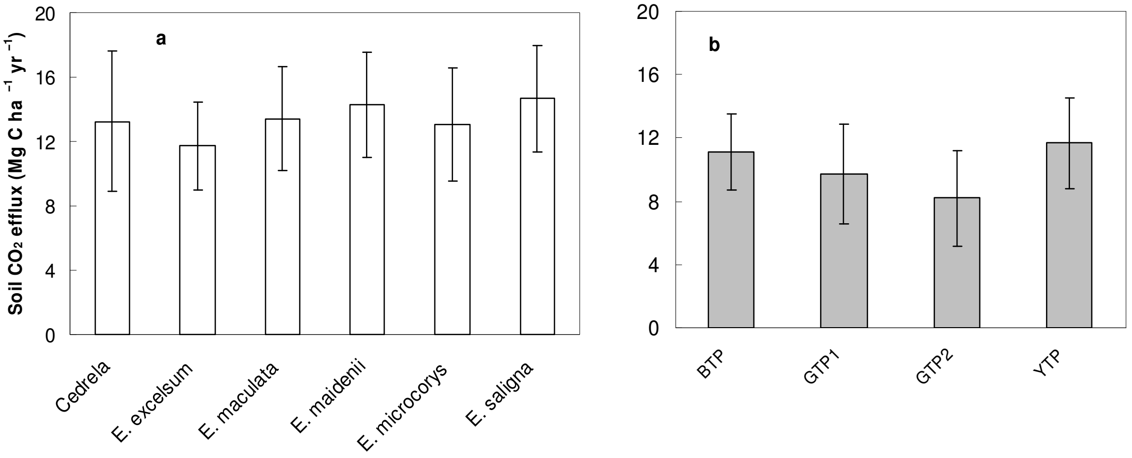

Figure 5. Mean annual soil CO_2 efflux from the (a) Ruhande monospecific stands and (b) the Nyungwe forest (Data from **Papers II** and **IV**). Vertical bars indicate standard deviation from the mean. Mean annual soil CO_2 efflux was highly variable with average coefficient of variation of 25.5% in the Ruhande monospecific stands and 28.8% in the Nyungwe forest sites. Abbreviation of site names: blue trail plot (BTP), green trail plot 1 (GTP1), green trail plot 2 (GTP2) and yellow trail plot (YTP).

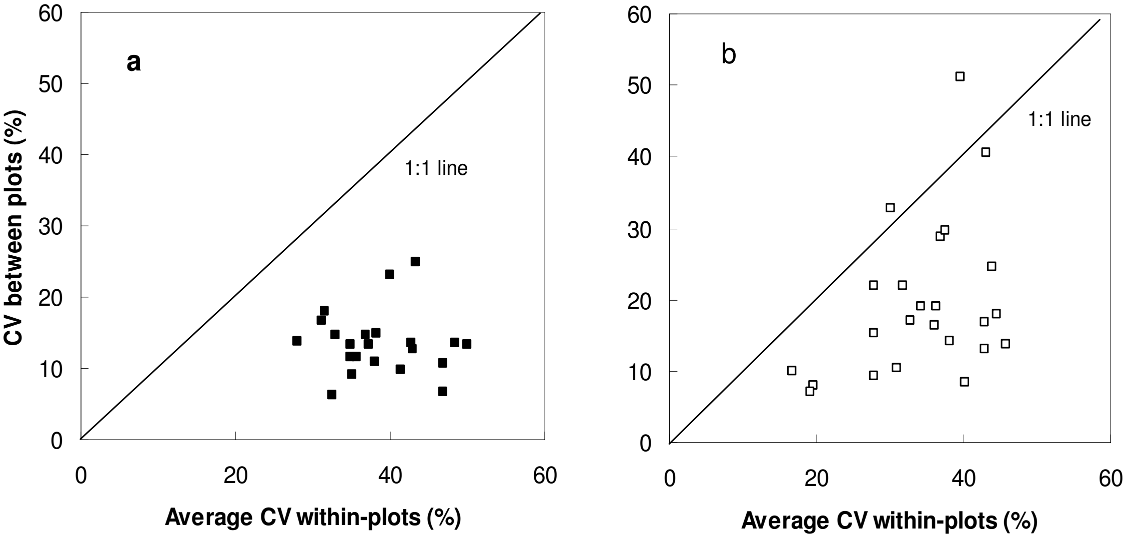

Figure 6. Coefficients of variation between plots *versus* average CV within-plots in the Ruhande Arboretum (a) and the Nyungwe forest (b). Within-plots variation was higher than the between plots variation at both sites (Data from **Papers II** and **IV**).

Table 2. Summary of soil CO_2 efflux studies in the tropical regions. Abbreviations: soil CO_2 efflux (SCE), soil temperature (T_s), soil water content (SWC), leaf area index (LAI), precipitation (P), soil organic carbon (SOC), soil carbon stock (Soil C), soil bulk density (BD), basal area (BA), root biomass (RM), aboveground litter (AGL).

Reference	Ecosystem type, Region	T_s (oC)	SWC (m^3 m^{-3})	P (mm)	Mean annual SCE (Mg C ha^{-1} y^{-1})	SCE range (Mg C ha^{-1} y^{-1})	Determinants of seasonal SCE	Determinant of diurnal SCE	Determinants of spatial SCE	Soil C (Mg C ha^{-1})	Forest density (trees ha^{-1})	Aboveground biomass (t ha^{-1})	LAI (m^2 m^{-2})	Altitude (m)
Davidson et al. 2000	Primary forest, Amazon	22–24		1800	20		P, SWC							
Davidson et al. 2000	Secondary forest, Amazon			1800	18		P, SWC							
Davidson et al. 2000	Active pasture, Amazon	23–31		1800	15		P, SWC							
Davidson et al. 2000	Degraded pasture, Amazon			1800	10		P, SWC							
Sotta et al 2004	Amazon	25–26	0.2–0.41	2200	24.4	16.4–36.9	SWC	T_s				300-350	5–6	
Salimon et al. 2004	Secondary forest, Amazon	23–33		1940	16		P, SWC			15				
Salimon et al. 2004	Mature forest	20–26		1940	17		P, SWC			14				
Salimon et al. 2004	Pasture	22–35		1940	24		P, SWC			25				
Epron et al. 2006	Primary forest, French Guiana	25.6	0.1–0.4	2980	16.2	8.4–24.5			RM, SOC, BD, T_s, pH				7.0	
Schwendenmann et al. 2003	Primary forest, Costa Rica	21–27	0.25–0.65	4200	10.7	10–16.6	SWC							150
Chambers et al. 2004	Amazon, Brazil		0.15–0.65	2380	12.1	7.9–15.5	Ts, SWC							100
Epron et al. 2004b	*Eucalyptus* plantation, Congo	25–30	0.03–0.11	1200		6–21.3	SWC, Ts		AGL		700		1.6	100
Epron et al. 2006b	*Eucalyptus* plantation, Congo	25–32	0.03–0.15	1170	15.7	7.6–30.4	P, SWC				530	105		100
Nouvellon et al. 2008	Savannah afforestation, Congo	23–32	0.05–0.12	1216	6.6	3–11	SWC			5				100
Hashimoto et al. 2004	Primary forest, Thailand	10–24	0.2–0.5	1657	25.6		SWC							1300
Adashi et al. 2006	Primary forest, Malaysia	24.3	0.18	2341	19.8		SWC		RM			403		
Adashi et al. 2006	Secondary forest, Malaysia	25.5	0.15	2341	20		SWC		Soil C, N					
Kosugi et al. 2007	Primary forest, Malaysia	24–26	0.2–0.44		14.8	9.5–24.7	SWC		SWC					
Janssens et al. 1998	Primary forest, French Guiana	24.9	0.16	2200	8.7				RM				8.6	
Janssens et al. 1998	Plantation, French Guiana	25	0.16	2200	11				RM					
Janssens et al. 1998	Clear-cut, FrenchGuiana	26.3	0.9	2200	9.5			T_s						
Bréchet et al. 2009	Forest plantation, French Guiana			3041	15.2	12.9–17			AGL, BA				3.9	

The spatial variation of soil CO_2 efflux at both sites (**Papers II** and **IV**) was high, with within-plots variation being higher than the variation between plots (Fig. 6). The averages within plots CV were 38.6% in the Ruhande Arboretum (**Paper II**) and 34.5% in the Nyungwe forest (**Paper IV**), while the averages between plots CV were 13.5% in the Ruhande Arboretum (**Paper II**) and 19.5% in the Nyungwe forest (**Paper IV**) (Fig. 6). These values indicate high error rates in the estimation of annual soil CO_2 emissions. High spatial variation in soil CO_2 efflux was also reported in other tropical studies (the range of CV was between 15–73%: Schwendenmann et al., 2003; Epron et al. 2004b; Epron et al., 2006a; Kosugi et al., 2007). Spatial variability of soil CO_2 effluxes in the Ruhande and the Nyungwe forest sites is explained by soil C and N stocks, basal area, aboveground biomass, soil pH and stand age (**Papers II** and **IV**). Effects of these factors on spatial variation of soil CO_2 efflux were also observed in other tropical forests (e.g., Epron et al., 2006a; Bréchet et al., 2009; Table 2). Correlation of soil C and N stocks with soil CO_2 efflux was also observed in tropical Asia and America (Salimon et al., 2004; Adachi et al., 2006; Epron et al., 2006a; Kosugi et al., 2007) and suggests the influence of substrate availability on soil respiration rate. Nitrogen content also determines the rate of litter decomposition (Luo and Zhou, 2006) and root biomass (Kosugi et al., 2007), and consequently the rate of soil respiration. Differences between soil CO_2 efflux in the Ruhande Arboretum (**Paper II**) and the Nyungwe forest (**Paper IV**) can be attributed to differences in climate, especially temperature which influences the rate of litter decomposition, microbial and plant metabolic activities, and consequently, soil CO_2 production and release (Xu and Qi, 2001; Luo and Zhou, 2006; Raich et al., 2006).

4.5 Seasonal variations of soil CO_2 efflux

The seasonal patterns of soil CO_2 efflux in the Nyungwe forest (**Paper IV**) and the Ruhande monospecific forest plantations (**Paper II**) were similar but the monthly mean soil CO_2 effluxes in the Ruhande Arboretum were 11 to 37% higher than those in the Nyungwe forest (Fig. 7). Seasonal variations of soil CO_2 efflux followed the pattern of precipitation and were highest in rainy seasons and lowest in dry seasons, mainly in July and August (Fig. 7; **Papers II** and **IV**). Soil CO_2 efflux increased with increasing soil water content but appeared to saturate or decrease above a soil water content of 0.25 m^3 m^{-3} in the Ruhande sites (**Paper II**) and 0.28 m^3 m^{-3} in the Nyungwe sites (**Paper IV**).

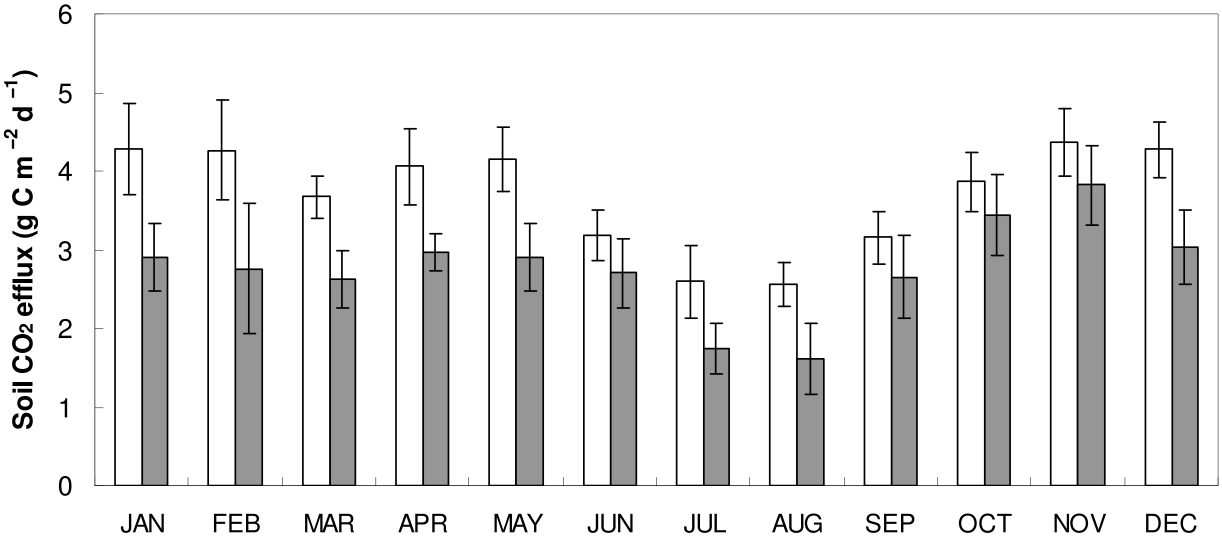

Figure 7. Seasonal variation in soil CO_2 efflux from January to December in the Ruhande Arboretum and the Nyungwe forest (Data from **Papers II** and **IV**). Symbols: white bars = Ruhande Arboretum, grey bars = Nyungwe forest. Error bars indicate standard deviation from the mean. Monthly mean is the monthly averages of all stands at the same site for 2 years (Ruhande Arboretum: 2006 and 2007; Nyungwe forest: 2007 and 2008).

Soil water content was the main driving factor in seasonal variation of soil CO_2 efflux in the Ruhande Arboretum (**Paper II**: R^2 = 0.36–0.77) and Nyungwe forest (**Paper IV**: R^2 = 0.41–0.75), which was also observed in tropical forests in America, Asia and Africa (Table 2; Epron et al., 2004a, b; Hashimoto et al., 2004; Salimon et al., 2004; Sotta et al., 2004; Kosugi et al., 2007; Werner et al., 2007; Nouvellon et al., 2008). The seasonality of soil CO_2 efflux associated with precipitation patterns and soil water content was also observed in tropical forests in Kenya, Thailand, Congo, Malaysia and Amazon (Table 2; Davidson et al., 2000; Epron et al., 2004b; Hashimoto et al., 2004; Salimon et al., 2004; Epron et al., 2006b; Kosugi et al., 2007; Werner et al., 2007; Nouvellon et al., 2008). High soil CO_2 efflux during the rainy seasons was attributed to increase in microbial and root activities in response to soil water content increase (Lee et al., 2002; Luo and Zhou, 2006). Conversely, low rates of soil CO_2 efflux in dry seasons when soil water content is low, is attributed to low substrate diffusion and water stress imposed on roots and microorganisms, which consequently reduce their metabolism and CO_2 production (Xu and Qi, 2001; Janssens and Pilegaard, 2003; Davidson et al., 2006)

The decrease in soil CO_2 efflux above a soil water content of 0.25 m^3 m^{-3} (**Paper II**) or 0.28 m^3 m^{-3} (**Paper IV**) was suggested to be attributed to a decline in oxygen and CO_2 diffusion in a water-saturated soil (Davidson et al., 1998, 2000; Xu and Qi, 2001; Rey et al., 2002; Valentini, 2003), and a decline in soil temperature caused by soil water content increase (Schwendenmann et al., 2003; Adachi et al., 2006; Epron et al., 2006a).

Variation in soil temperature exerted a minor effect on the seasonal variation of soil CO_2 efflux at the Ruhande sites ($R^2 = 0.06 – 0.17$; **Paper II**) while it exerted a relatively significant effect in the Nyungwe forest ($R^2 = 0.15 – 0.62$; **Paper IV**). Other studies have also observed that influence of soil temperature on seasonal variation in soil CO_2 efflux was smaller than that of soil water content in forest plantations in Congo (Epron et al., 2004b) and in tropical forests of Amazonia, Thailand and Malaysia (Davidson et al., 2000; Hashimoto et al., 2004; Salimon et al., 2004; Adachi et al., 2006). This is attributable to small soil temperature variability over the seasons. In contrast to tropical regions, influence of soil temperature on soil CO_2 efflux is very high in temperate and boreal forests due to wide range of seasonal and diurnal variations in temperature in those regions, which make it easier to observe changes in soil CO_2 efflux (Davidson et al., 1998; Xu and Qi, 2001; Rey et al., 2002; Curiel Yuste et al., 2003; Valentini, 2003; Mo et al., 2005; Tang et al., 2005; Gaumont-Guay et al., 2006; Wang et al., 2006).

Influences of soil water content and soil temperature in soil CO_2 efflux are indicative of their role in the production of soil CO_2 by influencing the physiological activities of plant growth and substrate supply, root respiration and microbial decomposition through the facilitation of enzymes and substrate diffusion. They also influence the transport of CO_2 in soil (Ouyang and Zheng, 2000; Schwendenmann et al., 2003; Valentini, 2003; Jassal et al., 2004; Luo and Zhou, 2006; Schwendenmann and Veldkamp, 2006; **Papers II, III** and **IV**).

4.6 Diurnal patterns of soil CO_2 efflux

Diurnal patterns of soil CO_2 efflux and soil temperature in stands of *Eucalyptus maculata* and *Entandrophragma excelsum* were associated in a bimodal pattern: a daytime phase that followed the variation in soil temperature, and a nighttime phase that was decoupled from the variation in soil temperature and most likely influenced by the supply of photosynthetic products (Fig. 2 and Table 2 in **Papers III**). The bimodal pattern of diurnal soil CO_2 efflux was also observed in Nyungwe forest (Fig. 4a in **Paper IV**). Diurnal variations of soil CO_2 efflux *versus* soil temperature described a counter-clockwise hysteresis loop (Fig. 4 in **Paper III**; Fig. 4b in **Paper IV**). Similar figures were also observed in an oak-grass savanna and boreal forests (Tang et al., 2005; Gaumont-Guay et al., 2006; Carbon and Vargas, 2008; Vargas and Allen, 2008b) and in a tropical forest (Janssens et al., 1998; Vargas and Allen, 2008a). Diurnal patterns of soil CO_2 efflux delayed to those of soil temperature. Previous finding indicated that the delay of soil CO_2 efflux to soil temperature results from the delay of soil CO_2 production, which is regulated by the supply of photosynthetic products to roots that occurs some hours later from the time of photosynthesis (Tang et al., 2005; Gaumont-Guay et al., 2006; Carbon and Vargas, 2008; Vargas and Allen, 2008a).

5. CONCLUSIONS AND FUTURE DIRECTIONS

- **Aims I and II**

The climate at the Ruhande Arboretum differed from that in the Nyungwe forest. The carbon stocks in the Ruhande Arboretum were higher than those in Nyungwe forest, and were dominated by the above-ground carbon stock which occupied 70% in the Ruhande Arboretum and 57% in the Nyungwe forest. The mean annual litter production was 3.4 Mg C ha^{-1} yr^{-1} and was 25% of annual soil CO_2 efflux at the Ruhande Arboretum. Litter production rate followed a seasonal pattern with lowest values during wet seasons and highest values in dry seasons.

- **Aims III and IV**

Mean annual soil CO_2 efflux in the Ruhande Arboretum (13.5 Mg C ha^{-1} yr^{-1}) and Nyungwe forest (10.2 Mg C ha^{-1} yr^{-1}) were comparable to those in other tropical forests. Seasonal variations in soil CO_2 efflux at our sites followed the pattern of precipitation and soil water content. Similar patterns were observed in other tropical forests in America, Asia and Africa. Spatial variations of soil CO_2 efflux from the Ruhande Arboretum and the Nyungwe forest were mainly explained by the variability in soil C and N stocks. Diurnal patterns of soil CO_2 efflux followed a bimodal pattern, describing a hysteresis effect with soil temperature and most likely affected by the transport of photosynthetic products. Hysteresis between diurnal soil CO_2 efflux and soil temperature was also noted in other tropical, boreal and temperate forests.

- **Future directions**

Further studies are needed before we can calculate the Rwandan carbon balance. Comparative to what has been advanced in other continents, future studies may explore: (i) the estimation of carbon stocks and fluxes associated with other land uses and other Rwandan forest types; (ii) separating autotrophic and heterotrophic components of soil respiration and their responses to seasonal and diurnal changes in soil temperature and soil water content; (iii) the influence of litter biomass, soil physical properties, and plant photosynthetic activity on total soil CO_2 efflux; (iv) long term soil CO_2 efflux dynamics through long term studies that will document the annual variations and potential effects of climate change on soil CO_2 efflux; and (v) the estimation of respiration and photosynthesis of the aboveground tissues.

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