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PH.D. THESIS

Carbon and Nutrient Cycling in Afromontane Tropical Forests at Different Successional Stages

Brigitte Nyirambangutse

DEPARTMENT OF BIOLOGICAL AND ENVIRONMENTAL SCIENCES

UNIVERSITY OF GOTHENBURG

Carbon and Nutrient Cycling in Afromontane Tropical Forests at Different Successional Stages

Brigitte Nyirambangutse

UNIVERSITY OF GOTHENBURG

Department of Biological and Environmental Sciences
Faculty of Sciences

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This doctoral thesis in Natural Sciences, specializing in Environmental Sciences, is authorized by the Faculty of Science and will be publicly defended on the 9th December 2016, at 10:00 h, in the lecture hall at the Department of Biological and Environmental Sciences, Carl Skottsbergs gata 22B (Botany Building), Gothenburg, Sweden.

Opponent: Professor Yadvinder Malhi
School of Geography and the Environment
University of Oxford
United Kingdom

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Nyungwe forest (photo Johan Uddling)

Supervisor: Dr. Göran Wallin
Co-supervisors:
Assoc. Prof. Johan Uddling
Prof. Håkan Pleijel
Assoc. Prof Donat Nsabimana
Assoc Prof. Elias Bizuru

Examiner: Professor Leif Klemedtsson

To You my bundles of joy, Maika and Nika and my beloved Husband Ephraim,

Et en mémoire de Toi Maman et Papa,

J'aurais tant aimé que vous soyez présents.

"…The birds were singing in trees and everywhere. It was very warm; a thunderstorm appeared on the horizon and soon there was thunder and lightning. We had to hurry to shelter. But the storm was soon over and the clear sky appeared..."
Then sings my soul, my Saviour God, to Thee;
How great Thou art, how great Thou art!

Carl Gustav Boberg
(1859-1940)

Abstract

To date, studies of the carbon and nutrient cycling in tropical montane forests have been restricted to a few, mostly neotropical, sites. This thesis investigated the carbon and nutrient cycling of early (ES) and late (LS) successional forest stands in Nyungwe forest, one of Africa's largest remaining tropical montane forests. The stocks and fluxes of carbon and nutrients, as well as the factors controlling these, were studied in 15 forest plots established within this PhD project.

Paper I explored forest carbon dynamics and demonstrated that Afromontane tropical forests contain large amounts of carbon, with the carbon stocks of LS stands being higher than those reported for tropical montane LS forests in South Asia and Central and South America. The total C stock was 35% higher in LS compared to ES stands due to significantly larger aboveground biomass (AGB), but productivity did not differ between the two successional stages. Differences in species composition and stem properties (wood density, height:diameter relationship) explained the differences in AGB between ES and LS forest stands.

Paper II investigated canopy nutrient cycling. It was found that neither leaf nutrient concentrations (exception: K) nor nutrient resorption efficiencies during senescence differed between ES and LS species. Furthermore, total leaf litterfall and its content of C, N, P and K did not differ between ES and LS stands. Mean resorption efficiencies of N (37%), P (48%) and K (46%) were much higher than for other nutrients. Nutrient resorption efficiency exhibited a very large interspecific variation which was not related to the leaf concentration of the respective element. High leaf N concentrations, intermediate N:P ratios, and low resorption efficiencies compared to values reported for other TMF together indicate high fertility and likely co-limitation by N and P in this forest.

Paper III showed that interspecific variation in photosynthetic capacity among tropical montane trees was related to within-leaf N allocation rather than to total area-based leaf N content. While ES species had higher photosynthetic capacity (+58 to +67 %), dark respiration (+41%) and photosynthetic quantum yield (+38%) than LS species, the two groups did not significantly differ in total leaf N content, chlorophyll content or leaf mass per unit area.

Paper IV investigated the spatial and temporal variation in soil CO_2 efflux and found that the daytime variation correlated with soil temperature while the nighttime variation did not. Spatial variation in soil CO_2 efflux was strongly related to soil C and N content.

The results demonstrate that Nyungwe montane forest contains large amounts of carbon (especially in LS stands) and have high productivity. The thesis also shows that accounting for the effects of forest disturbance on stand structure, especially species composition, substantially improves the estimations of carbon stocks. Furthermore, it contributes to the understanding of these forests by elucidating which factors that control tree growth, photosynthetic capacity and soil CO_2 efflux. The findings of this thesis contribute to reducing a large knowledge gap regarding the carbon and nutrient stocks and dynamics of African tropical montane forests at different successional stages.

Keywords: Tropical montane forest, Africa, Nyungwe, Successional stage, Carbon stock, Net primary production, Photosynthesis, Soil CO_2 efflux, Nutrient cycling

List of Papers

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

Nyirambangutse B., Zibera E., Uwizeye K. F., Nsabimana D., Bizuru E., Pleijel H., Uddling J. and Wallin G. Carbon stocks and dynamics at different successional stages in an Afromontane tropical forest, *Biogeosciences Discuss*., doi: 10.5194/bg-2016-353, 2016, in review.

Nyirambangutse B., Zibera E., Dusenge M.E., Pleijel H., Uddling J. and Wallin G. Canopy nutrient cycling in Afromontane tropical forests at different successional stages. *Manuscript*

Ziegler C., Dusenge EM, Nyirambangutse B, Wallin G., Uddling J. Controls of interspecific variation in photosynthetic capacity in tropical Afromontane rainforests tree species. Submitted to *Tree Physiology*

Nsabimana D., Zibera E., Ibáñez T.S., Nyirambangutse B., and Wallin G. Spatial and temporal variation of soil CO_2 efflux in tropical montane forest stands in Central Africa. *Manuscript*

The papers and their respective supplementary material are appended at the end of the thesis.

Abbreviations and Symbols

AGB	Aboveground biomass
BGB	Belowground biomass
C	Carbon
C_i	Intercellular CO_2 concentration (µmol mol^{-1})
CO_2	Carbon dioxide
$[CO_2]$	Carbon dioxide concentration (µmol mol^{-1})
CR	Coarse roots
CWD	Coarse woody debris
D	Diameter at breast height (cm)
DIC	Dissolved inorganic carbon
DOC	Dissolved organic carbon
ES	Early successional species
FR	Fine roots
GPP	Gross primary productivity
H	Tree height
K	Potassium
LS	Late successional species
J_max	Maximum rate of photosynthetic electron transport (µmol m^{-2} s^{-1})
LMA	Leaf mass per unit area (g m^{-2})
N	Nitrogen
NEE	Net ecosystem exchange
NEP	Net ecosystem production
NPP	Net primary production
P	Phosphorus
R_A	Autotrophic respiration
R_H	Heterotrophic respiration
V_cmax	Maximum rate of photosynthetic carboxylation (µmol m^{-2} s^{-1})
SOM	Soil organic matter
TMF	Tropical montane forest
VOC	Volatile organic compounds

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1 Introduction

1.1 Forests and climate change

The rise in atmospheric CO_2 concentration, [CO_2], due to the burning of fossil fuels and its effects on climate has renewed interest in the study of the global carbon (C) cycle (Watson et al. 1990). Atmospheric concentrations of the greenhouse gas CO_2 has increased 40% since 1750, the onset of industrial era, from 278 ppm to 402 ppm in 2016 (Ciais et al. 2013, Le Quéré et al. 2013, Fig 1). The main causes of this increase are combustion of fossil fuels (coal, gas, oil), production of cement and land use change activities, mainly deforestation (Ciais et al. 2013). Global C budgets from the last decade shows that about 27% of the past anthropogenic CO_2 emissions are stored in terrestrial ecosystems, with a similar amount stored in oceans, while the remaining fraction has caused the increase in atmospheric [CO_2] (Fig. 2, Le Quéré et al. 2013). This increase is predicted to continue during the coming decades at a rate depending on the development of emissions from combustion of fossil fuel and land use change (Le Quéré et al. 2015), and on the response of terrestrial ecosystems to climate change (Brienen et al. 2015). Deforestation in the tropics is one of the key sources of CO_2 emissions (Pan et al. 2011) but tropical ecosystems, mainly forests, are also important sinks (Brienen et al. 2015). De Vries (2014) argued that declining global forest sinks potentially could accelerate the rate of [CO_2] increase by 50%.

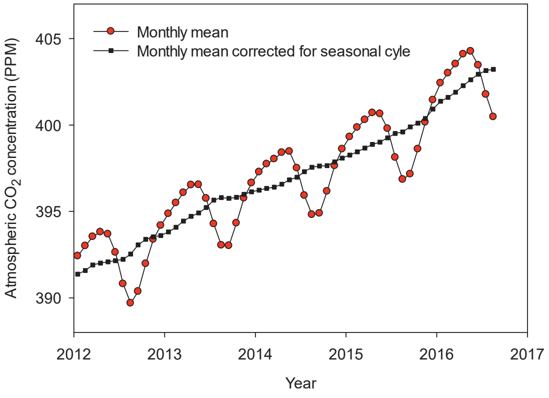


Figure 1. Recent monthly mean [CO_2] globally averaged over marine surface sites. The red symbols represent monthly mean values, centered on the middle of each month. The black symbols represents the same, after correction for the average seasonal cycle (Dlugokencky and Tans 2015).

Since the first IPCC report (IPCC 2990), there has been a considerable increase of research on the role of forests in the global C cycle. Forests are potential major stocks and major sinks of CO_2, given their spatial extent, biomass and productivity (Malhi et al.

1999, Malhi & Grace 2000). Tropical forests play an important role in controlling the global C cycle and, thus, the rate of ongoing climate change (Lewis 2006, Stocker et al. 2013). They store more than half of the C in the world's forests (Pan et al. 2011), and provide roughly one-third of the global terrestrial primary production (Beer et al. 2010). However, most research has been focused on the Neotropical forest area, the largest tropical forest area, while little has been conducted in the second largest tropical forest area of Central and West Africa (Malhi et al. 2013). Due to the globally uneven distribution of research on forest C cyling, the size and location of the terrestrial C sinks and C storage remains uncertain (Pan et al. 2011, Saatchi et al. 2011). One of the largest uncertainties is that regarding the estimates of aboveground biomass (AGB, Saatchi et al. 2007), which accounts for approximately 75% of total net primary productivity (NPP) in tropical forests, while only 63% in temperate forests and 54% in boreal forests (Malhi et al. 2015a). The spatial and temporal variability of AGB depends on factors such as climate, human and natural disturbance and recovery, soil type, and topographical variations (Saatchi et al. 2007).

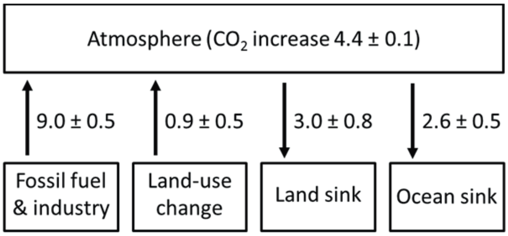


Figure 2. Average of global net C budget for the period 2005 - 2014. The arrows represent emissions from fossil fuels and industry, emissions from deforestation and other land-use change, the growth of CO_2 in the atmosphere, and the uptake of CO_2 by the land and ocean. All fluxes are in units of Gt C yr^{-1} (modified from illustration by Le Quéré et al. 2015).

1.2 Forests and succession

"*Primeval tropical rain forest, undisturbed and stable, 'since the dawn of time' is a myth"* (Chadzon 2003)

FAO (2010) defines primary forests as forests of native species in which there is no clear visible sign of past or present human activities. These are estimated to occupy 36% of the total forest area, while secondary forests occupy 57 % (FAO 2010). Over half of the world's tropical forests are not old-growth forests but rather regenerating forests (Chadzon 2003, Poorter et al. 2016). It is therefore a large source of uncertainty to consider forests as pristine and uniform in structure when in reality they represent a mosaic of successional patches, reflecting the frequency, intensity and scale of natural or anthropogenic disturbances over time. Stand structure and floristic composition often differs between secondary and primary forest, also denoted old-growth forests (Chadzon 2003). However, definitions of secondary forests in the literature are vague and ambiguous. In this thesis, the terms early (ES) and late (LS) successional forest stands are used instead of secondary and primary forest, to emphasise that succession is a continuous process rather than a two-step process after natural or anthropogenic disturbances (Grace et al. 2014).

Pan et al (2011) subdivided tropical forests into two categories: *intact* (here: LS) and *regrowth* (here: ES); and attribute almost 70% and 30 % of the total tropical forest area to each category, respectively. Tropical LS forests absorb approximately 25% of global forest net uptake of atmospheric CO_2 every year (Malhi 2010, Pan et al. 2011) reducing rate of increase in atmospheric CO_2 (Malhi 2010). However, as a consequence of ongoing global change, as disturbances and drought continue to increase mortality of trees, LS tropical forests can shift from being C sinks to becoming net C sources (Lewis et al. 2011, Brienen et al. 2015).

The magnitude of the tropical C sink is relatively well known for LS forest (Pan et al. 2011, Saacthi et al. 2011), but current global estimates of C uptake and storage of ES forests are uncertain (Pan et al. 2011, Saatchi et al. 2011). ES forests play an important role in the provision of ecosystem services such as C sequestration, hydrology regulation, and biodiversity conservation. Although these forests commonly contain less C per unit area compared to intact forests (Berenguer et al. 2014), they nevertheless must be considered in any attempt to make a comprehensive analysis of the C fluxes.

In the context of the United Nations initiative to reduce emissions from deforestation and degradation (REDD+), accounting of carbon requires accurate estimation of C stocks and associated changes in land use. Large variation in C stocks among regions highlights the need for local estimates of forest C (Saatchi et al. 2011) to reduce the uncertainties due to data scarcity (Pan et al. 2011), especially from the African continent (Malhi et al. 2013).

Disturbance, natural or human-made, is likely to alter forest potential for C storage in ways that are not yet completely understood (Wright 2010). Moreover, the rate at which ES forests will recover and provide equivalent levels of ecosystem services as the forests they replaced remains highly uncertain (Poorter et al. 2016). The extent to which C stock is degraded in ES tropical forests depends on the type of disturbance (such as logging, fires) as well as its intensity and frequency (Berenguer et al. 2014). Disturbance regime has been reported as a key factor in determining tree species composition, diversity and community structure and heterogeniety (Laurance et al. 2006). In terms of species composition, disturbances lead to the establishment of early successional plant communities, composed mostly by light demanding species (Peña-

Claros 2003). These species are characterized by low wood density and stature with high relative growth rate compared to late successional species (Lawton 1984). However, as they inherently grow faster (Quilici and Medina 2998, Poorter et al. 2008), C stocks and productivity are consequently affected during succession. Despite the progress made in quantification of both biomass and productivity in tropical LS forests, ES forests have been overlooked.

1.3 Forests and cycling of carbon

Reliable predictions of the role of tropical forests in the global C cycle and how they will be affected by climate change requires understanding of how C storage and fluxes vary across time, among environmental conditions and forest types. To understand this, studies of the compartmental fluxes and stocks in major forest ecosystem types are essential (Clark et al 2001).

Plants remove CO_2 from the atmosphere through photosynthesis, known at ecosystem level as gross primary production (GPP). Carbon fixed into plants is then cycled through plant tissues, litter and soil C and can be released back into the atmosphere by autotrophic (plant, R_A) or heterotrophic (soil microbial and animal, R_H) respiration (Fig.3). Additional losses occur from foliage as volatile organic carbon (VOC). The sum of belowground fraction of R_A and R_H is called soil respiration (R_s). The difference between GPP and R_A plus VOC is considered as plant growth and at ecosystem level referred to as net primary production (NPP):

$$\mathrm{NPP} = \mathrm{GPP} - R_A - \mathrm{VOC} \qquad (1)$$

In practice, NPP is measured as the total new organic matter produced in a specified time interval and area (e.g. Mg C ha^{-1} yr^{-1}) such as production of different ecosystem biomass components according to:

$$\mathrm{NPP} = \mathrm{Wood}_{inc} + L_{canopy} + L_{FR} \qquad (2)$$

where Wood_{inc} is increment of above and below ground wood (stem, branches, coarse roots), L_{canopy} is litterfall from the canopy (leaf, fruits, twigs etc) and L_{FR} is the litter production of dead fine roots (≤ 2 mm diameter). Hence, estimates of NPP are based on measurements of growth of different plant organs rather than on measurements of CO_2 exchange and the terms in Eq. 2 may also be determined as NPP components (NPP_{wood}, NPP_{canopy}, $\mathrm{NPP}_{fine\ roots}$). NPP also includes components that are more difficult to measure such as carbon lost through herbivory, carbohydrate exudates from roots or transferred to mycorrhizae and parasites. Failure to account for these fluxes is the reason why NPP estimates are commonly substantially underestimated (Clark et al. 2001).

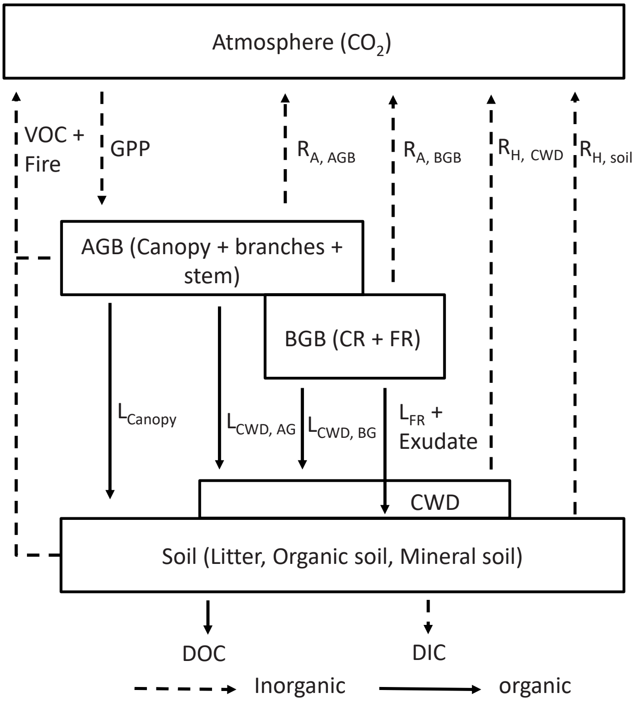


Figure 3. Schematic illustration depicting the major components of the C balance in forest ecosystems. GPP (Gross primary production) is partitioned to aboveground biomass (AGB) including canopy, branches and stems; to belowground biomass (BGB) including coarse roots (CR) and fine roots (FR); and to autotrophic respiration (R_A). Dead material from AGB and BGB produces litter from canopy (L_{canopy}), fine roots (L_{FR}) and coarse wood debris (L_{CWD}) supplying the soil with organic material that will be decomposed (after month to thousands of years storage) by soil microorganisms through heterotrophic respiration (R_H). Furthermore, C will be lost from AGB and BGB as carbohydrate exudates from roots or transferred to mycorrhizae. Additionally, C will be lost from the ecosystem as volatile organic compounds (VOC) and fire products (mainly CO_2) emitted to the atmosphere; and as dissolved inorganic C (DIC) and dissolved organic C (DOC) in drainage to rivers and lakes.

Eventually the woody components will die and form coarse wood debris (CWD) which will be transferred to litter and together with canopy and litter production of dead fine roots form soil organic matter (SOM), which successively will be decomposed by animal and microbial organisms during a process referred to as heterotrophic respiration (R_h). The difference between NPP and R_h is the net ecosystem exchange (NEE) of C with the atmosphere:

$$\mathrm{NEE} = \mathrm{NPP} - R_H \quad (3)$$

Subtracting also the C losses through dissolved organic carbon (DOC) and dissolved inorganic carbon (DIC) gives the net ecosystem production (NEP):

$$\mathrm{NEP} = \mathrm{NPP} - R_H - \mathrm{DOC} - \mathrm{DIC} \quad (4)$$

Finally, part of the NEP may be lost through disturbances such as harvests, erosion and combustion in natural or human-induced fires. Accounting for this yields the net biome production (NBP) which is the long term storage of C in ecosystems:

$$\mathrm{NBP} = \mathrm{NEP} - \mathrm{Disturbance} \quad (5)$$

Prior estimates of NPP have been based on direct measurements of a few major NPP components. A couple of frequently measured components are aboveground NPP (i.e. (stem + branches) and foliage NPP (Chambers et al. 2001, Malhi et al. 2004). It is only since recently that some studies have presented comprehensive data on all components of respiration, GPP and NPP (Malhi et al. 2009, Girardin et al. 2014). Such data have become increasingly available through the development of permanent networks of intensive monitoring sites, such as the Amazon Forest Inventory Network (RAINFOR, Malhi et al. 2002, Phillips et al. 2009, http://www.geog.leeds.ac.uk/projects/rainfor/), the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA, Avissar & Nobre 2002), the Andes Biodiversity and Ecosystem Research Group (ABERG, Malhi et al. 2010), and the Global Ecosystem Monitoring network (GEM, http://gem.tropicalforests.ox.ac.uk/) across the Amazon basin, Africa and Asian tropics where NPP is continuously quantified. However, belowground production quantification has been lagging behind although the plots in GEM/ABERG networks include assessments of fine root production (Girardin et al. 2013, Malhi et al. 2015b).

1.4 Estimation of biomass C pools

The aboveground biomass (AGB) pool has been reported to be the one most affected by human-induced disturbances (Berenguer et al. 2014). This pool has been the focus of forest inventories in intact forests (e.g. Phillips et al. 1998, Lewis et al. 2009) and estimates of C stocks are based on allometric relationships between AGB and stem diameter and height as well as data on wood density (Clark et al. 2012). A range of pan-tropical allometric equations have been developed for mixed tree species in various forest types and bioclimatic zones that use a variety of variables and algebraic forms (Mattsson et al. 2016). The earlier equations were mainly based on stem diameter while progress has been made towards including a more reliable scaling (Brown 1997, Chave et al. 2005, Chave et al. 2014) and wood density data compilation. Chave et al. (2005) combined data on stem diameter, tree height and wood density from 2412 harvested trees from many types of tropical forests to build equations for different forest types; dry, moist and wet. Chave et al. 2014 provided an improved allometric equation based on a larger dataset (including many ES forest tree species from wet, moist and dry forests). Tropical forests are known to be species diverse with between 40 000 and 53 000 tree species (Silk et al. 2015) and data on wood density is available only for 8412 taxa (Chave et al. 2009). Till now, the Chave et al. (2014) equations would be the best to use as they are the most recent and are based on the largest dataset so far, including also secondary forest tree species.

1.5 Tropical montane forests

Tropical montane forests (TMF) cover c. 8% (elevation > 1000 m a.s.l.) of the total tropical forest area (Spracklen and Righelato 2014) and are considered as specifically important for harboring biodiversity and water regulation (Martínez et al. 2009, Scatena et al. 2011). These biological hotspots are particularly vulnerable to climatic warming (Pounds, 1999, Still et al. 1999; Corlett 2012). However, field-based measurements of NPP and C budgets studies of tropical forests have largely focused on lowland forests. There have been far less studies in TMF compared to the large quantities of data put together in lowland tropical forests (Malhi et al. 2004, Aragao et al. 2009, Kho et al. 2013, Malhi et al. 2015b). Studies indicate that TMF has been underestimated with respect to its capacity to store (Spracklen and Righelato 2014) and sequester (Fehse et al. 2002) C.

Overall, estimates of GPP and NPP based on measurements in TMF are rare (Girardin et al. 2010, Malhi et al. 2016) and a few additional GPP and NPP estimates come from models (Marthews et al 2012). Consequently, questions regarding the environmental controls on GPP and NPP in TMF remain open. Elevational transect studies are in their early years (Girardin et al. 2010, Huasco et al. 2014, Girardin et al. 2014, Clark et al. 2015). Current understanding of the role of TMF in regulating global biogeochemical cycles is therefore hampered by the paucity of field data on productivity and soil C, but also on tree biomass, especially from the African continent (Malhi et al. 2013a,b, Spracklen and Righelato 2014). Thus, comprehensive assessments of ecosystem aboveground and belowground NPP are required to provide a complete picture of the functioning of these ecosystems and provide insights on how they will react to the projected changes in climatic patterns.

Forest productivity and the global C cycle are strongly constrained by nutrient availability (Fernandez-Martinez et al. 2014). Nitrogen (N) and phosphorus (P) are the two elements typically limiting net primary production (NPP) in terrestrial ecosystems (Chapin 1980, Vitousek et al. 2010), Some evidence suggests that N limitation may be common in montane tropical forests while lowland tropical forests with weathered soils are more limited by P (Tanner et al. 1998) although other elements may also be important (Kaspari et al. 2008). Several studies have demonstrated that productivity of many TMF is limited by nutrient availability via lower inputs of nutrients (or increased nutrient outputs) and slower cycling of nutrients (Benner et al. 2010) especially the latter. It has been suggested that reduced temperatures, excess soil water, reduced solar radiation, strong winds are the main causes of slower nutrient cycling in tropical montane forests.

This incomplete understanding has global implications given the importance of tropical forests for the global C cycle and climate. Thus, understanding the ways in which these forests cycle C and nutrients is critical for accurately predicting how these forests may respond to many threats of natural or human perturbations (Towsend et al. 2011).

2 Scope

The main objective of this thesis is to increase the understanding of the stocks and dynamics of C and nutrients in an Afromontane tropical forest, and explore possible differences between forest stands at different succession stages. This work, presented in four papers, was conducted by biomass inventories, measurements of leaf and soil CO_2 exchange, analyses of C and nutrients in leaves, litter and soil, and meteorological measurements in fifteen 0.5 ha plots in Nyungwe tropical montane forest in Rwanda. The specific aims are as follows:

Paper I examines the carbon stock, relative growth rate (RGR), and NPP of early (ES) and late (LS) successional forest stands using data from inventories of quantitatively important ecosystem compartments.

Paper II assesses leaf concentration and resorption of 12 elements (macro- and micro-nutrients) in ten early and ten late successional tree species and the canopy cycling and soil turnover of carbon and nutrients at stand scale.

Paper III addresses the importance of different chemical and structural leaf traits in controlling the interspecific variation in photosynthetic capacity among 12 tropical montane forest tree species belonging to ES or LS groups.

Paper IV explores the spatial (meters to km) and temporal (diurnal to seasonal) variations of soil CO_2 efflux in relation to abiotic factors and forest successional stages.

3 Material and Methods

3.1 Study site and disturbance history

The studies was conducted in the Nyungwe tropical montane forest (hereafter “Nyungwe”) which is a national Park in south-western Rwanda located between 2°17´-2°50´S, 29°07´-29°26´E at elevations ranging from 1600 to 2950 m a.s.l. and cover an area of 1013 km^2 (Fig. 4). Together with the contiguous Kibira National Park in Burundi, it is an important biodiversity hotspot that forms Africa’s largest remaining block of montane forests. It is a mixture of secondary and primary forest stands (Fashing et al. 2007) due to its disturbance history (see Plumptre et al. 2002, Masozera and Alavalapati 2004, Masozera et al. 2006). Nyungwe was first established as a forest reserve in 1933 (Weber 1989, Masozera & Alavalapati 2004). Although it was under protection, Nyungwe was still exploited with the rights to cut valuable hardwoods and collect firewood without any monitoring plan. This led to an increase in other anthropogenic activities within the forest such as honey collection, hunting, gold mining, small scale agriculture (Weber 1989). A buffer zone of fast growing exotic pine and eucalyptus plantations as a boundary of the forest and source of wood for local communities was established along the entire border of the forest. In 1997-98, eastern part of Nyungwe was affected by massive fires, and more than 12 800 hectares (approximately 12% of the park) was burned (WCS 2011). Additionally, about 30 to 50 hectares are burned every year as results of human activities. The forest gained National Park status in March 2004 (Gross-Camp et al. 2012)

Across all plots used in this study the mean annual air temperature ranged from 14.1 and 16.1°C and the mean annual precipitation ranged between 1657 to 3016 mm (see paper I) with a pronounced dry season from mid June to mid August. Further details of the plots are presented below and in paper I-IV.

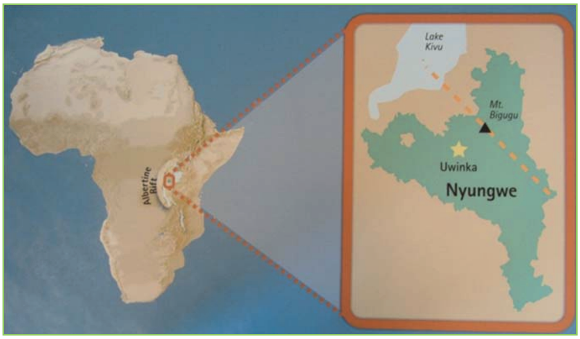


Figure 4. Study site: Map of Nyungwe forest showing the location of highest point (Mt Bigugu 2950 m a.s.l.) and the main center for tourism and research (Uwinka) where our long-term meteorology station is located.

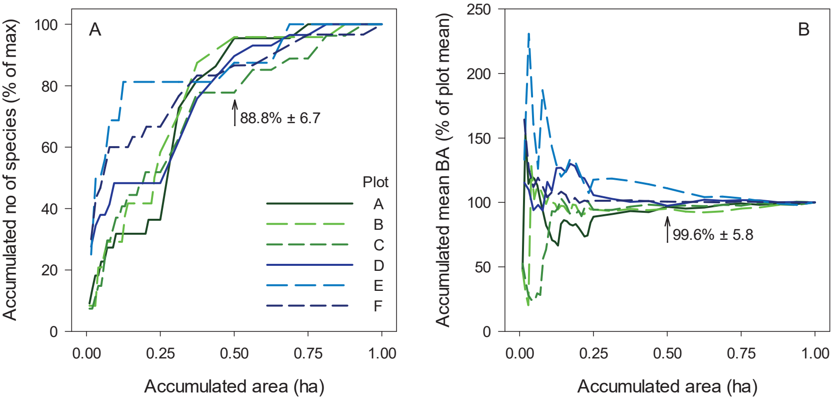


Figure 5. Species (a) and basal area (BA) (b) accumulation curves in a total area of 1 ha for each curve. Each plot was divided into subplots with 16 (12.5 m x 12.5) in one quadrant and 4 (25 m x 25 m) in other quadrants. Plot A - C is ES plots and D - F is LS plots. Stems having a *D* ≥ 5 cm were included.

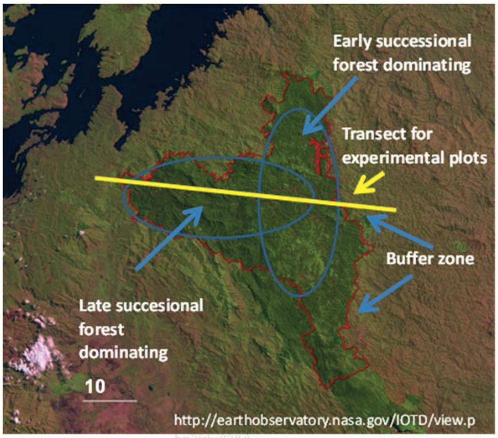
3.2 Pilot study

Since plot size is important for unbiased estimates of forest biomass (Chave et al. 2003), a pilot study was conducted between July 2011 and December 2011 to determine required plots size for this study, before establishing long-term plots. The pilot study included six 1 ha plots (100 m x 100 m) used to pre-survey species composition and basal area to establish information on minimum plot area to include a representative sample of both species and biomass. Each stem within the plots with a diameter at breast height (*D*) > 5 cm was identified to species whenever possible, and its D was recorded. Occasional unknowns were identified only to genus. The six plots included three dominated by ES species and three dominated by LS species. Each plot consisted of nested quadrats of 100 m^2, 625 m^2, and 2500 m^2 to facilitate establishment of species and biomass accumulation curves (Fig. 5). The results showed that the accumulated number of species in percentage of the total number of species in 1 ha were reaching almost 90%, and the curves from the two successional groups approached each other, at a plot area of 0.5 ha (Fig. 5a). The basal area accumulation curves stabilised already at approximately 0.25 ha, corroborating with previous recommendations using a minimum plot size of 0.25 ha for estimation of AGB in tropical forests (Chave et al. 2003).

3.3 Set up of Long-term plots

Based on the results from the pilot study, fifteen 0.5 ha plots were established during December 2011 to June 2012. They were arranged along an East to West transect of 32 km within Nyungwe, to include various forest stands, including stands at different successional stages (Fig. 6). Plots were located at an elevation between c. 1950 to 2500 m a.s.l. They were rectangular (100 m x 50 m, planimetric) and each plot was divided into 8 subplots (25 m x 25 m, in total 120) to facilitate sampling design etc.

Each subplot corner was marked with wooden poles, and a tree (stem) map of each plot was constructed. Upon establishment, the first census was launched following the same procedure for species identification and stem *D* measurements as in the pilot study. In case of trees with buttresses *D* was measured above the buttress at a known point of measurement. A second census was conducted from late 2014 to mid 2015, after approximately 3 years, when stem diameter were re-measured as well as new recruits and tree mortality was recorded.



http://earthobservatory.nasa.gov/IOTD/view.p

Figure 6. Experimental design: East-Western transect of plots.

3.4 Classification of stands into successional groups

The plots were classified into ES and LS groups to test for different features of C and nutrient cycling in forest stands of different successional stages. This classification was used in all four studies (Paper I – IV) and is presented in detail in Paper I.

Based on the results from the first census, each plot was classified into successional groups. A successional index (SI), ranging from 0 to a maximum of 1, was developed to classify the successional stage of the plots from the fractions of ES and LS tree species within the plots:

$$\mathrm{SI_x} = \frac{\mathrm{LS_x}}{\mathrm{T_x}} \times \left(1 - \frac{\mathrm{ES_x}}{\mathrm{T_x}}\right) \qquad (6)$$

where T is the plot total. The subscript x denotes if it is based on basal area (BA) or number of tree individuals (#). The index was based on the 10 most abundant species representing on average 77% of the basal area and 59% of the individuals of all plots. Based on this index, two groups of five plots each were defined, one with the lowest (< 0.1) and one with the highest $\mathrm{SI_x}$ (> 0.5), denoted ES and LS plots, respectively. The remaining five plots had an index ≥ 0.1 to ≤0.5 and were classified as intermediate successional plots (MS). The MS plots were included when data were averaged for the whole study, but not in analysis of differences between successional groups. Similar ranking and grouping resulted if the index was based on number of stems instead.

3.5 Measurements

Measurements were conducted on all 15 plots (6.5 ha) to study the above and below ground C stock, NPP as well as relative growth rates (RGR) of trees (Paper I). Furthermore, measurements of nutrient cycling (Paper II), photosynthesis (Paper (III) and soil CO_2 efflux (Paper IV) were conducted on all plots. The photosynthesis and nutrient cycling was focused on the most abundant ES and LS tree species. All studies were focused on important stocks and fluxes of C presented in Fig. 3, while nutrient cycling was focused nutrients in leaves, leaf litterfall and soil. However, C stocks and fluxes related to CWD and emissions of VOC, DOC and DIC were not measured, nor GPP, the R_A of above ground vegetation and NPP of understory vegetation, which prevent a closure of the total C balance. The methods for the measurements are presented in details in paper I to IV and summarised below and in Table 1.

The C stocks were estimated in the following pools: AGB (live trees, understory vegetation), belowground biomass (i.e. fine roots and coarse roots) and soil (litter, organic and mineral soil). Stand level estimates of tree aboveground C stocks were obtained from *D*, height, wood density and C content by using an allometric equation (Chave et al. 2014). Coarse root biomass was calculated based on stem biomass. Fine root biomass and soil C content was estimated from samples of litter, organic soil and mineral soil (Table 1). The soil and fine roots in each fraction was separated for determination of C and N content in soil (Paper I, II, IV) and fine root biomass (Paper I), respectively. Canopy litterfall (leaves, flowers, fruits, twigs, epiphytes) was monitored using litter traps distributed in each plot using a randomised block design (Paper I, II). To monitor RGR, dendrometer bands were installed using a randomised block design (considering distribution over all plots and stem *D* classes) on trees of two most abundant ES (*Macaranga kilimandscharica*) and LS (*Syzygium guineense*) species (Paper I). Fine root growth was estimated using ingrowth cores harvested 3 times over 1.5 years. NPP was determined based on measurements of wood C stock increment in two census, fine root growth, and canopy litter (Paper I).

Leaf and litter nutrient concentrations (12 elements) were measured in green mature leaves from the canopy and litter collected from the litter traps, respectively, representing 20 of the most abundant ES and LS species. Based on these measurements, the nutrient resorption efficiencies and litterfall recycling of nutrients were estimated. The resorption was calculated using equations accounting for leaf mass loss and leaf area shrinkage during senescence (Paper II).

Light-saturated photosynthetic rate was measured in sunny exposed leaves, using a portable photosynthesis system. Response curves of assimilation vs internal leaf CO_2 were used to estimate maximum Rubisco activity, V_{cmax}, and potential electron transport rate, J_{max}, using a set of leaf photosynthesis model equations (Paper III). Measurements of leaf structural and chemical traits (Table 1) were conducted to assess their influence on the variation in photosynthetic capacity.

To quantify soil CO_2 efflux (SCE, representing R_A and soil R_H) respiration in both ES and LS stands, temporal (T-study) diurnal and seasonal) variation was assessed in four 24 m x 24 m plots and spatial (S-study) variation was assessed in all 15 plots, using soil CO_2 exchange chambers. Data from the T-study was collected in 2007-2008, while the data from the S-study was collected in 2014-2015. Temperature, soil water content and pH were measured at all positions to assess its influences on SCE (Paper IV).

3.6 Meteorological measurements

Weather stations were installed along the transect of the plots to collect data of air temperature, relative humidity, radiation, precipitation. One climate station was established in February 2007 at Uwinka research site (Nsabimana 2009) and three minor stations were installed in June 2013. Soil temperature and moisture was measured at two of the stations. At the center of each plot, air temperature and humidity was also recorded. Detailed information is found in Paper I.

Table 1. Overview of methods and sampling periods for studies of C and nutrient cycling in the plots of Nyungwe tropical montane forest, including both above and below ground compartments (see next two pages).

Component/ parameter	**Description**	**Sampling period**	**Sampling interval**
Aboveground	**Aboveground wood biomass** was determined by using the allometric equation by Chave et al. 2014 based on stem diameter, wood density and tree height (Paper I):		
Coarse wood C stock & NPP	**Stem diameter:** All trees ≥ 5 cm diameter at breast height (*D*) was measured using diameter tape. For trees with major irregularities (e.g. buttresses) at breast height, the point of measurements (POM) was moved upwards and *D* was calculated using a taper function from Metcalf et al., 2009 (Paper I).	2011/12 -	~3 years
	Wood density: Wood cores for wood density calculations were sampled from most abundant tree species using an increment borer. For the remaining species, data was obtained from the global wood density data set (Chave et al., 2009; Zanne et al., 2009; Paper I).	2014/2015	Once
	Tree height (H): A species specifc *H* vs *D* relationship was established by measuring *H* of 930 trees, representing the full *D* range of the most abundant species using a clinometer (Vertex IV, Haglöfs Sweden AB, Långsele, Sweden). The H vs D relationship was used to determine tree H of all individuals, were the average relationship was used for the less abundent species (Paper I).	2013/2015	Once
	Recruitment & Mortality rate: New and dead trees were recorded in census 2 compared to census 1 (Paper I).	2011/12 - 2014/15	~3 years
	Diameter growth rate was determined by dendrometer bands installed on two most abundant species (*Macaranga kilimandscharica* and *Syzygium guineense*; Paper I).	May/July 2012 - Jan 2016	Every third month
Understory vegetatio C stock	**Biomass** of all understory vegetation with a *D* < 5 cm (woody, herbaceous and grass species) was determined by harvest from three square meter plot randomly placed at one of 16 grid points within each subplot using a 5 x 5 m grid. All plants within the one square meter plots were harvested at ground level and thereafter dried in 70 °C until constant mass, from which the dry mass per area of understory was calculated (Paper I).	2014	Once
Fine litter NPP	**Litterfall** was collected in 0.3 m^2 litter traps, placed 1 m above the ground surface in six of out of eight subplots in each plot (# 90). The location was randomly assigned among 16 grid points within each subplot using 5 x 5 m grid. The litter was dried in 70 °C until constant mass, separated into leaves, reproductive organs (fruits, flowers, seeds), twigs, epiphytes, and unidentified fine debris, and weighed. (Paper I and II)	2013-2014	Every second week
Leaf litter Nutrient cycling, resorption	**10 senecsed leaves** of the four most abundant species were selected from litter samples, oven-dried at 70 °C to constant mass. Discs were taken and measured to estimate the leaf area shrinkage. Nutrient concentrations were determined (Paper II).	2013/14	

Table 1. Continued

Component/ parameter	**Description**	**Sampling period**	**Sampling interval**
Fresh leaves Nutrient limation, resorption	**Fresh adult leaves** were sampled from up to 20 m height of the canopy to evaluate their nutrient concentrations. Five leaves per species were collected. Samples were weighed, dried to constant mass, ground . Foliar nutrient concentrations were determined. Discs were taken and measured to estimate the shrinkage (Paper II).	2013/14	Once
Photosynthetic capacity	Responses of net photosynthetic rate to air CO_2 concentrations (A-C_i curves), to photosynthetic photon flux density (PPFD) and dark respiration were measured on a total of 116 mature sun exposed leaves (one per tree) taken from 12 species. Other leaf traits such as LMA (leaf mass per area), thickness, SPAD values, Chl content, total Nitrogen concentrations and leaf biochemical photosynthetic capacity (V_{cmax} and J_{max}, the maximum rate of carboxylation and electron transport capacity, respectively) were d (P III)	2015	
Belowground Coarse wood C stock & NPP	**Coarse roots biomass** was not measured directly but rather estimated from aboveground coarse wood carbon stocks (Paper I)	2014-2015	once
Fine roots C stock & NPP	**Fine roots biomass**: fine roots defined as ≤ 2 mm were extracted from each sample of organic and mineral layers (Paper I)	2014-2015	Once
	Fine roots NPP: Ingrowth cores were installed in the center of each subplot of each plot to 40 cm depth. Roots were removed manually from the soil samples in four 7 to 8 minutes intervals and stored in plastic bags in cumulative pattern ,then washed,analyzed , dried at 70◦C ,and weighed to get the cumulative mass (Metcalfe et al 2007). Organic and mineral horizons were separately taken into account and root free soil was reinserted into the ingrowth core and re introduced back into soil (Paper I).	2014-2015	Every three to four months
Soil C & N stock	Samples of forest floors and soil were taken from 480 sampling locations. Organic soil (O) was excavated from a 0.5 x 0.5 m ground area. Mineral (M) soil 0-15 cm, 15 cm - 30 cm, and 30 cm - 45 cm layers were sampled using a soil auger. Fresh mass were weighted. 20% subsample was taken from O samples. M-samples from each subplot were mixed. Roots were removed. Soil samples were oven-dried at 70 °C until constant mass, milled in a ball mill and C concentrations were determined thereafter by dry combustion, using an elemental analyzer (Paper I and II, IV)	2014-2015	once
CO_2 efflux	**Soil CO_2 efflux** was measured using a closed chamber. Permanent collar made of PVC tubes were installed in advance (4 months) at three positions in each subplot (360 positions in total, spanning all 15 plots). Air and soil temperatures were measured with a thermistor probe. Soil water content was recorded with a soil moisture sensor. Additional measurements were made before (2007-2008) in four (25 x 25 m) plots in Nsabimana (2009) study (Paper IV)	2007-2008 and 2014/15	

4 Results and Discussion

4.1 Biomass and carbon stocks

While ES forest stands with closed canopy and mature trees had significantly lower AGB and BGB (59%, $P = 0.023$ and 52%, $P = 0.025$, respectively) than LS stands, there were no significant differences observed for the soil C stock (Paper I). The stem biomass was also found to be significantly ($P < 0.001$) correlate with the successional index. As a consequence, the plant (AGB + BGB) fractions of the total C stock was significantly lower in ES compared to LS plots (32% in ES, 54% in LS; $P = 0.020$). This finding is in line with other studies reporting relatively unaffected soil C stocks in moderately disturbed and secondary tropical forest (Martin et al. 2013; Marin-Spiotta et al. 2009). However, the total C stock in above and belowground C pools estimated to 299 and 402 Mg C ha^{-1} in ES and LS plots, respectively, was not significantly different ($P = 0.11$; Table 4 in paper I).

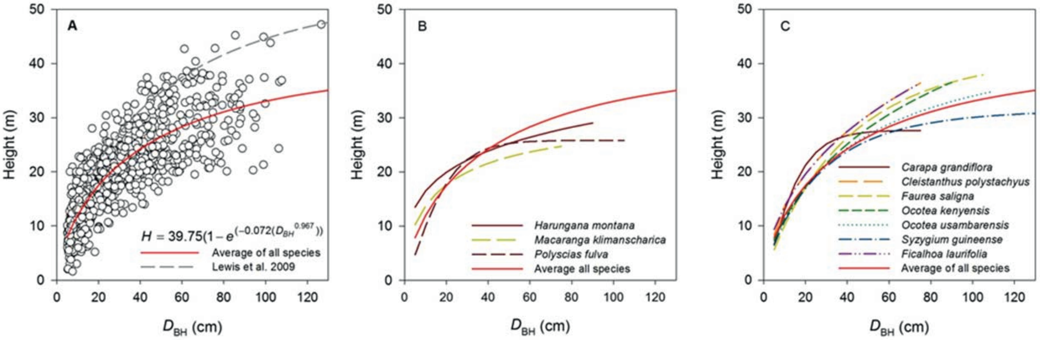


Figure 7. Height (H) vs stem diameter at breast height D relationship for 930 trees representing the 25 most abundant species of all plots and fitted to equation in (a). The relationship for all measurements (red line) is compared to the measurements of 1982 trees in African tropical forests (Lewis et al. 2009, grey dashed line) mainly at an altitude below 1000 m a.s.l (a) as well as to species-specific functions for the 10 most abundant species, including (b) three ES species and (c) seven LS species (Paper I).

The lower C stock in AGB at ES stands can be attributed to a different forest structure, where trees in LS stands had considerably higher wood density and height vs diameter relationship (in larger size classes) compared to ES tree species (Fig.7). It was found that the dominant ES species *M. kilimandscharica* rarely grows taller than 25 m (Fig 7b), and that mature LS trees were significantly taller than mature ES trees at a given tree diameter. ES stands are composed of pioneers, with low stature and light wood (Muller-Landau 2004). Consequently, species composition, together with associated differences in wood density and allometry between ES and LS tree species are largely explaining the significantly lower C stock in secondary forests. While the stem biomass was found to significantly correlate with the successional index, the soil C pool was not affected by successional status. Other studies have reported similar soil C pools in secondary and primary forests (Martin et al. 2013;) but a meta-analysis study has shown contradictory results that secondary forests stored less soil C than primary forests (Don et al. 2010). Estimates of C stocks in different pools are presented in Table 4 of Paper I.

4.2 AGB C stock in Nyungwe compared to other tropical forests

To explore if African TMFs have higher C stocks compared to TMF in South America, data were compiled from studies of AGB (trees with $D > 10$ cm) of old-growth tropical lowland forest (< 1000 m a.s.l.) and TMF (elevations: 1600 to 2800 m a.s.l. and mean annual temperature: 11 to 18 °C, c. ± 300 m and ± 2.5 °C of our lowest and highest elevation and temperature, respectively; (Table 2; Paper I). While acknowledging the limited sample sizes for African tropical montane forests, it was found that the late successional (LS) stands of Nyungwe TMF had higher AGB than the average old-growth lowland tropical forests in 10 Central/East Amazonia forests (+11%) and a bit lower than lowland forests in Central Africa (-11%) and in Borneo (-15%; Table 2). Average stem density, basal area and wood density in our LS stands were similar to those observed in lowland tropical forests. These findings support the suggestion by Spracklen and Righelato (2014) that TMF biomass may store more C than earlier expected and also show that AGB of late successional (LS) plots was substantially higher in African TMF compared to TMF in Southeast Asia and Central and South American. These results are consistent with the view from Ensslin et al. (2015) that the general pattern of higher AGB in Africa than in lowland rainforests of America may hold in TMF. Based on few available data on belowground C stock (Delaney et al. 1997; Grimm and Fasbender, 1977; Girardin et al. 2010; Moser et al. 2011), we found that belowground C stock (soil C fraction in the LS plots was 51%) is similar to the levels reported in these studies, however due to inconsistent sample methodologies, and sampling depth, the similarity occur only after adjusting for differences in sampling depth

4.3 NPP in Nyungwe compared to other TMF

Total NPP (NPP_{TOTAL}) was on average 9.41 ± 1.50 Mg C ha^{-1} yr^{-1} and is slightly lower than the reported average NPP for lowland tropical forests (Malhi et al. 2011). There was no difference between ES and LS plots, and this is likely due to the counteracting effects of differences in stem biomass and relative growth rate of both successional stages (Paper I).

Table 2. Above ground biomass (AGB) and forest structure (including trees with *D* > 10 cm) of old-growth tropical lowland (< 1000 m a.s.l) and montane forest of different tropical regions. The TMF sites were selected to be within an altitude range of 1600 to 2800 m a.s.l. and an annual mean temperature range of 11 to 18 °C. The mean, min and max values are based on the mean from sites. Abbreviations: SE, South-east; C & E, Central and East; C, Central; MAT, mean annual temperature, MAP, mean annual precipitation, *D*, breast height diameter; BA, basal area; ρ, wood density (Paper I)

	Tropical Lowland Forest									Tropical Montane Forest									
	SE Asia[a]			C & E			C Africa[c]			SE Asia[d]			C & S America[e]			C & E Africa[f]			This study[g]
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Elevation (m a.s.l.)	249	9	-991	122	41	-197	456	35	-874	2205	1560	-2825	2208	1750	-2825	2347	2230	-2464	2230
MAT (°C)	26	22	-27	26	25	-27	25	22	-27	15	12	-18	14	11	-18	14	12	-15	15
MAP (mm)	3127	2052	-4441	2421	2009	-2856	1853	1530	-2837	2468	1891	-3985	2976	1487	-5000	2281	2240	-2322	2322
AGB (Stems, *D* ≥ 10 cm	456	196	-779	341	251	-387	431	147	-749	248	119	307	224	78	408	327	275	380	380
BA (m ha^{-1})	37	22	-49	29	23	-34	32	14	-47	41	34	-53	36	27	-51	42	35	-49	35
ρ (g cm^{-3})	0.60	0.56	-0.64	0.68	0.65	-0.72	0.64	0.45	-0.84	0.58	0.56	-0.61	0.54	0.52	-0.56	0.62			0.62
Stem density (ha^{-1})	584	326	-1337	597	-		426	181	-650	1467	697	-2943	1343	477	-2753	428	378	-478	478
No of sites/plots/total area (ha)	56/79/235			4/17/29			51/193/253			4/19/3			8/52/12			2/10/4			1/5/2.5

[a] Slik et al. (2010) - (Borneo – Brunei; Malaysia; Indonesia).

[b] Baker et al. (2004); Quesada et al. (2010); www.ctfs.si.edu/group/Ecosystems+and+Climate/Data+Resources - (Brazil).

[c] Lewis et al. (2013) - (Cameroon; Central African Republic; Democratic Republic of Congo; Gabon; Nigeria; Republic of the Congo).

[d] Aiba et al. (2005); Clumsee et al. (2010); Dossa et al. (2013); Edwards and Grubb (1977); Kitayama and Aiba (2002); Sawada et al. (2016) - (Malaysia and Indonesia; Papua New Guinea). ρ and stem density only from 3 sites.

[e] Alvarez-Alteaga et al. (2013); Delaney et al. (1997); Delaney et al. (1998); Girardin et al. (2010); Girardin et al. (2014); Grimm and Fassbender (1981); Lieberman et al. (1996); Moser et al. (2011); Leuschner et al. (2007); Spracklen et al. (2005); Unger et al. (2012) - (Costa Rica; Ecuador; Mexico; Peru; Venezuela). BA, ρ and stem density only from 3 sites.

[f] This study; Ensslin et al.(2015); Rutten et al. (2015b); Hemp (2006) - (Rwanda; Tanzania). ρ only from this study.

[g] Only LS plots, stems with *D* ≥ 10 cm.

To put results from Nyungwe into perspective, published data were collated from a review by Malhi et al. (2011) on aboveground (NPP_{AG}) and total (NPP_{Tot}) net primary productivity in tropical forests and plotted against elevation of each study (Fig. 8). The compilation clearly showed that productivity decrease with increasing elevation as shown by earlier studies (Kitayama and Aiba 2002; Girardin et al. 2010), and that Nyungwe had both higher NPP_{AG} and NPP_{Tot} compared to sites at similar elevation (Fig. 8). Different studies have attempted to explain factors controlling NPP in tropical forests. High rainfall > 3000 mmm yr^{-1} and low temperature reduce NPP through reduced mineralization rates (Clark et al. 2001; Girardin et al. 2010). Both temperature and rainfall was similar in Nyungwe and other sites at similar elevations (not shown), therefore neither rainfall nor temperature could explain the high NPP in Nyungwe compared to other sites. Wood production, which is directly linked to NPP, has been demonstrated to vary positively with fertility across Amazonia (Malhi et al. 2004). It is therefore suggested that the high leaf nitrogen (N) concentration in this study (Table 1 in Paper II) compared to other tropical montane forests may explain the high NPP in the Nyungwe.

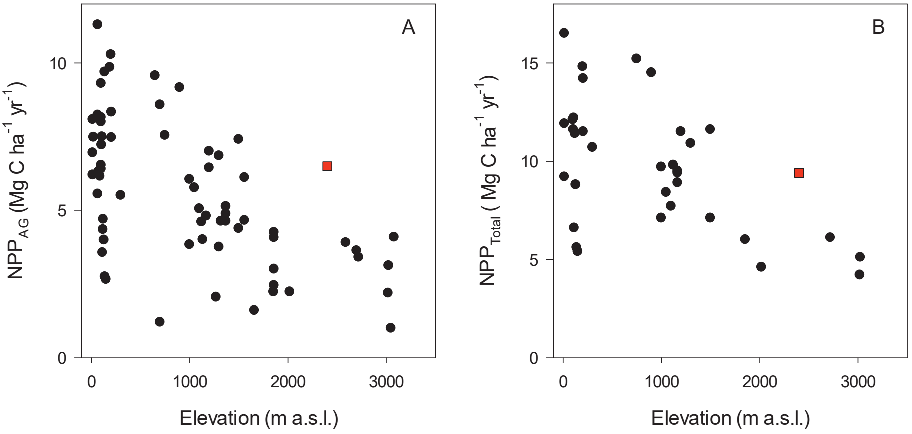


Figure 8. (a) The above ground (NPP_{AG}) and (b) total net primary productivity (NPP_{Total}) from different tropical forests (Malhi et al. 2011) compared to the mean NPP of Nyungwe. Black filled circle, published data; Red square, Nyungwe data.

4.4 Nutrient cycling

It was found that for all macro- and micronutrients except P, their ratios to N were mostly higher than or similar to the suggested optimal ratios (Linder et al 1995), which indicates that none of K, Ca, Mg, S, Fe, Mn, Zn or B were limiting tree growth in Nyungwe TMF (Paper II). While B and K were just slightly below the limiting ratio in three species, P was below the suggested optimal ratio range for P (8-10% of N) in 18 of the 20 studied species. Koerselman and Meuleman (1996) suggested somewhat different limits for the transition between N and P limitation, at N:P ratios between 14 and 16 (corresponding to P:N ratios of 6.3-7.1%). According to these limits, 11 species were P limited, 5 species N limited and 4 species co-limited by N and P, indicating overall co-limitation of N and P in Nyungwe forest, but with P being somewhat more limiting than N. Although TMF has been considered to be N limited (Vitousek and Sandford 1986) the results from fertilisation experiments in TMF indicate that some forest are limited by N, some by P, and other co-limited by both (Tanner et al. 1998, Benner et al. 2010 and references therein).

Nyungwe forest seems to be richer in N than other TMF, as we observed mean leaf N concentrations of 20.4 mg g^{-1} while other TMF studies found average values ranging from 10 to 18 mg g-1 (Vitousek and Sandford 1986; Paper II). For leaf P, however, values in our study are within the range found in these earlier studies (1.3 mg g^{-1} in our study compared to 0.5 – 2.1 mg g^{-1} in other studies).

Altough, significant (P <0.028) differences among species regarding leaf concentrations of all macro- and micronutrients, leaf nutrient concentrations (exception for K and Mg) did not differ between ES and LS species. However, there were significantly higher N:P ratios in LS compared to ES species (Table 2 in Paper II), indicating that the degree of P limitation is greater in LS than in ES stands. This significant difference was the combined result of small and statistically non-significant differences in leaf N and P content (Table 1 in Paper II).

Nutrient resorption differed significantly among species but independent of successional status. The average N, P and K resorption efficiencies (37%, 48 %, 46%; mass loss and leaf area shrinkage corrected) were lower than the global averages (62%, 65%, 70%) estimated by Vergutz et al. (2012). However, our results corroborate the general observation that resorption efficiency for nutrients other than N, P and K has a much lower efficiency (e.g. Vergutz et al. 2012). There was a large and significant inter-specific variation in NRE, PRE and KRE and it was not correlated with these elements concentrations in leaf. This is in line with other studies (Aerts 1996, Killingbeck 1996, Aerts and Chapin 2000) and was likely caused by inherent differences among species rather than differences in environmental conditions.

4.5 Nutrient flux in litterfall

Annual total litterfall ranged between 4.5 to 11.5 Mg ha^{-1} yr^{-1} and was in range of earlier observations in TMFs (3.6 - 11 Mg ha^{-1} yr^{-1}). The contribution of leaf litterfall was 67% of the total litterfall. Leaf litterfall peaked in the later part of the dry season during the first year (2013) as it has been observed in other studies (Cizungu et al. 2014, Paudel et al. 2015), but not during the second year (2014). This could be due to the fluctuations in precipitation between years (Paper II, Fig. 2).

The annual nutrient flux of N, P and K through litter was estimated to 90, 5 and 30 kg ha^{-1} yr^{-1}, respectively. This is in the upper range observed in several other TMF in South America and Africa (28-90, 1-5, 6-39 kg ha^{-1} yr^{-1} of N, P and K, respectively; Vitousek and Sandford 1986, Becker et al. 2015). It was also found that the average litter N concentration in the Nyungwe forest (average 15 mg g^{-1} and range 8 - 28 mg g-1) was high compared to most other TMF (6 – 1.2 mg g-1; Vitousek and Sandford 1986, Veneklaas 1991, Wood et al. 2011, Becker et al. 2015), suggesting enhanced mineralisation ability and nutrient availability. Overall the study suggests that Nyungwe forest is more fertile than many other TMF and thus support the observation of high NPP (Paper I).

4.6 Controls of differences in photosynthetic capacity

Net photosynthesis at light saturation and an intercellular CO_2 (A_{n280}), as well as photosynthetic capacity determined as V_{cmax} and J_{max} was significantly ($P \leq 0.010$) higher (59%, 58% and 67%, respectively) in ES compared to LS species (Figure 9). However, the two successional groups did not significantly differ in total leaf N content, chlorophyll content or leaf mass per unit area. The interspecific variation in photosynthetic capacity was not explained neither by the total leaf area-based nutrient content (Fig. 10a) nor LMA between the two groups and these results is in line with previous studies (Coste et al. 2005, Dusenge et al. 2015). This variation was related to differences in within-leaf nitrogen allocation, with a larger investment of leaf N into compounds maximizing photosynthetic capacity (Rubisco and bioenergetics (Fig. 10b). These results agreed with a recent global meta-analysis (Ali et al. 2015) which showed that within-leaf N allocation was much more important than total leaf N content in explaining variation in photosynthetic capacity.

ES species had higher dark respiration (+41%; $P = 0.004$; Figure 11a) and photosynthetic quantum yield (+38%; $P = 0.018$; Figure 11b) than LS species, The 41% higher R_d in ES compared to LS species agrees with a study on Bornean rainforest tree seedlings suggesting that R_d might be the most suitable physiological

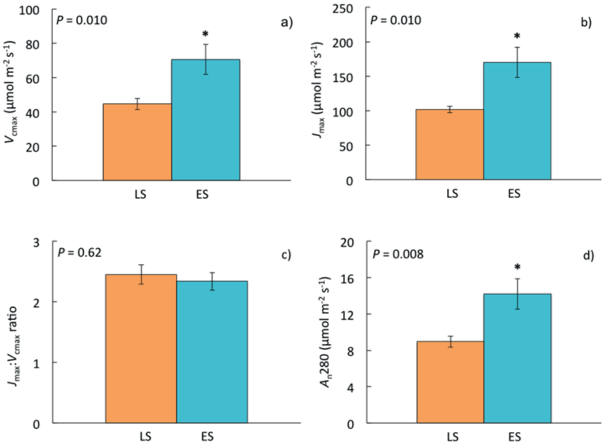


Figure 9. Maximum rates of (a) photosynthetic carboxylation (V_{cmax}) and (b) electron transport (J_{max}) as well as the (c) J_{max}:V_{cmax} ratio and the (d) light-saturated net photosynthesis at an intercellular CO_2 concentration of 280 μmol mol^{-1} (A_{n280}) of early-successional (ES) and late-successional (LS) tree species in Nyungwe forest. The P value of the t-test comparing successional groups is shown in each panel (Paper III).

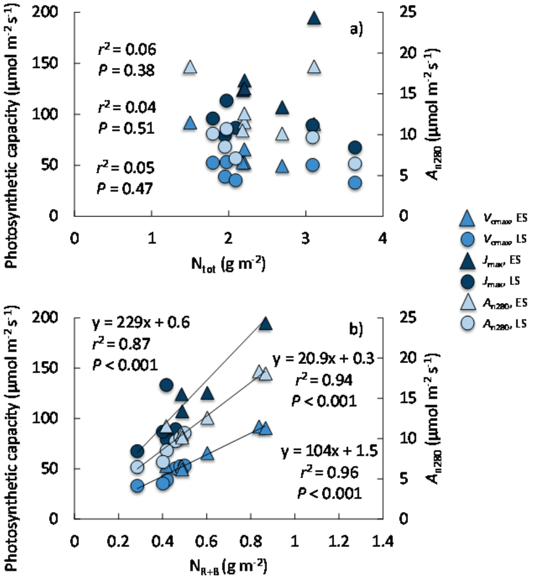


Figure 10. Photosynthetic capacity (V_{cmax}, J_{max}, A_{n280}) in relation to area-based (a) total leaf nitrogen content (N_{tot}) and (b) the leaf N content of compounds maximizing photosynthetic capacity (N_{R+B}), as well as (c) photosynthetic quantum yield (QY) in relation to the leaf N content of compounds involved in photosynthetic light-harvesting (N_{LH}; see equations 3, 4 and 5 for definitions of N_{R+B} and N_{LH}). Values of r^2 and P are shown for all relationships, while equations and regression lines are only shown for significant relationships ($P \leq 0.05$; Paper III).

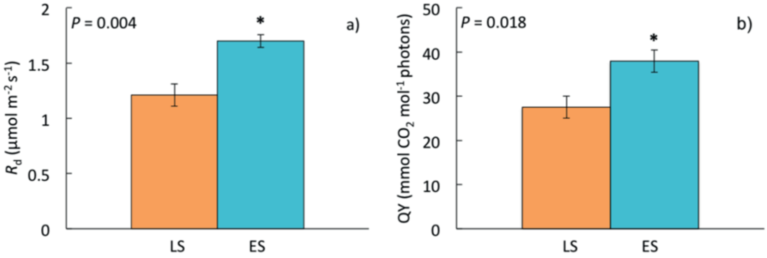


Figure 11. (a) Leaf dark respiration (R_d) and (b) quantum yield of photosynthesis (QY) of early-successional (ES) and late-successional (LS) tree species in Nyungwe forest. The P value of the t-test comparing successional groups is shown in each panel (Paper III).

leaf trait to indicate shade-tolerance (Baltzer and Thomas 2007). The higher photosynthetic quantum yield in ES conflicts with the C gain hypothesis which states that shade-tolerant LS species have plant traits that maximize C gain under low light conditions such as low respiration and LMA, high chlorophyll content and quantum yield of photosynthesis (Valladares and Niinemets 2008)

4.7 Mean annual and spatial variations of soil CO_2 efflux

The mean annual soil CO_2 efflux in Nyungwe was 15.1 ± 2.6 Mg C ha^{-1} yr^{-1} with a plot range from 9.9 to 19.4 Mg C ha^{-1} yr^{-1} (Paper IV) and was in the range of those observed in other tropical forests (Raich and Schlesinger, 1992; Schwendenmann et al. 2003; Sotta et al. 2004; Zhou et al. 2013). There was no significant difference between ES and LS forest stands.

On a global scale, SCE has been shown to be closely related to NPP (Raich and Schlesinger, 1992). Only marginally significant relationship with fine root and canopy NPP was observed in this study, and wood and total NPP did not correlate (Fig 12a). Instead, the SCE in this study was significantly related with soil C content (Fig. 12b) and N content (Paper IV, Fig S1; $R^2 = 0.48$; $P = 0.015$), suggesting that these soil traits explain the spatial variation in SCE. An increase in SCE with soil C stock was also observed in other forests ecosystem, suggesting the dependence of soil respiration on the availability of substrates to soil microorganisms (Epron et al. 2006a; Luo and Zhou 2006; Nsabimana et al. 2009). Sites with high N stock may also have high SCE due to positive effects of a large microbial biomass on decomposition and maintenance respiration (Kosugi et al. 2007; Luo and Zhou 2006), but since soil C and N are highly correlated ($R^2 = 0.87$) it is difficult to draw firm conclusions on which of the two elements that is the most important to explain the spatial variation in SCE.

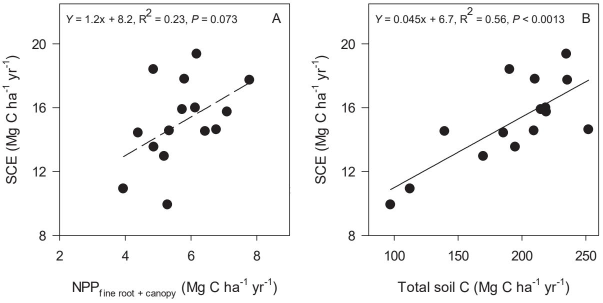


Figure 12. Annual soil CO_2 efflux (SCE) in relation to (a) NPP$_{\text{fine root + canopy}}$, (b) total soil C. Total soil includes ground litter, organic soil layer and mineral soil down to a depth of 45 cm in the mineral soil (Paper IV).

4.8 Seasonal and diurnal variation of soil CO_2 efflux

The seasonal pattern of SCE showed a sharp decline during July and August each year (Fig. 13) and mirrored the patterns of soil water content (SWC) and rainfall (Paper IV). SCE reached the highest rates during the rainy seasons and the lowest rates were measured in the dry season in July and August when the SWC was low (Figs. 1b, 3). Seasonal variation in SCE was most correlated to SWC (Paper IV, Fig. 5a; $R^2 = 0.41 - 0.75$) compared to temperature (Paper IV, Fig. 5b; $R^2 = 0.16 - 0.62$), increasing when SWC was between $0.17 - 0.28$ m^3 m^{-3}, and decreasing above a SWC of 0.28 m^3 m^{-3}. The temporal SCE patterns observed here are in line with observations from lowland tropical forest soils (Raich et al. 2002) but contrasts with the results from other high elevation studies indicating that there is no seasonality in soil respiration in high elevation soils (Bruijnzeel et al. 1998). The diurnal variation was relatively small (amplitude of 15%), but with a clear peak in the afternoon, resulting in a systematic overestimation of SCE by c. 5% if diurnal variation is not taken into account when calculating diurnal mean and seasonal means.

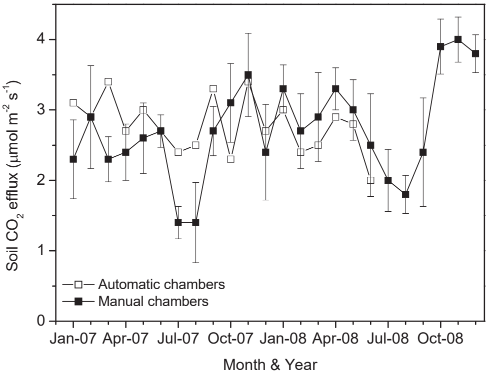


Figure 13. Seasonal variation in soil CO_2 efflux from January to December. Errors bars indicate standard deviation from the mean (Paper IV).

5 Key findings

In **paper I** it was shown that TMF contain large amounts of C. Late successional (LS) stands have higher AGB compared to early successional (ES) stands. This was attributed to differences in wood density and H to D ratio between LS and ES tree species. LS stands had higher AGB than their counterparts in South America. Stem biomass was significantly related to the successional index while the soil C pool was not affected by successional stage. Productivity was similar in LS and ES stands.

Paper II found that leaf N concentrations did not differ between ES and LS species. Nutrient resorption efficiency varied significantly among species but was independent of species successional identity. Resorption efficiencies of N, P, and K were higher compared to other macro- and micronutrients, but lower compared to recent estimates of nutrient resorption efficiency in global meta-analyses. Annual total litterfall was in the range of earlier observations in TMF. The annual nutrient flux of N, P and K through litterfall was in the upper range of fluxes observed in several other TMF in South America and Africa. High leaf N concentrations, intermediate N:P ratios, and low resorption efficiencies compared to values reported for other TMF together indicate high fertility and likely co-limitation by N and P in the study area.

Paper III examined the leaf traits controlling the interspecific variation in photosynthetic capacity of tropical montane trees. It demonstrated that interspecific variation in photosynthetic capacity is related to within-leaf N allocation rather than to total area-based leaf N content. While ES species had higher photosynthetic capacity, dark respiration and photosynthetic quantum yield than LS species, the two groups did not significantly differ in total leaf N content, chlorophyll content or leaf mass per unit area.

Paper IV reports on the spatial and temporal variation in soil CO_2 efflux (SCE). The mean annual soil CO_2 efflux in Nyungwe was in the range of those observed in other tropical forests. There was no significant difference between ES and LS forest stands. The SCE in this study was significantly related with soil C and N content, suggesting that these soil traits explain the spatial variation in SCE. The study also demonstrates that there is seasonality in soil respiration in TMF soils.

6 Outlook

The results presented in this thesis provide the most comprehensive synthesis to date of C and nutrient cycling in tropical montane forests of different stages of succession. Our findings refine estimates of average C stocks taking into account differences in wood density and allometry of species at early and late successional stages. The results can therefore be used to provide more accurate estimates of C stocks and fluxes for tropical forest C inventories, from regional to global scales.

In terms of C stocks, NPP, leaf nitrogen concentrations and seasonality in soil CO_2 efflux, Nyungwe appears to be different from other TMFs. However, we acknowledge that the results reported here represent only one study; other studies may show different results given that tropical montane forests are highly variable.

Moving forward, we anticipate that the results from this thesis will be of value for understanding and managing the role of tropical montane forests in the global C cycle. Specifically, the data will be useful to better understand tropical montane forest C stocks, fluxes, and productivity, how these are shaped by disturbance and how they are affected by other environmental factors. Some of the results (Paper III) will also be useful for model calibration and improvement and could be integrated in earth system and vegetation models. For example, accounting for differences in within-leaf N allocation, which was shown to be linked to species successional strategy, would improve the current vegetation models.

TMF soils store large amounts of C, possibly as a result of lower mineralisation rates due to lower temperature compared to lowland tropical forest. Since soil respiration was strongly linked to the amount of soil C, a future temperature stimulated soil respiration may lead to reduced C soil storage. On the other hand, rising temperatures may also lead to higher availability of N due to increased mineralisation, which may stimulate tree growth and production of litter. The net effect of these opposing processes is currently difficult to predict, which calls for further investigations.

This thesis presents a unique dataset where intensive monitoring of the C and nutrient cycles has been conducted across a series of 15 1/2ha plots along a succession gradient. This provides an opportunity to understand how the C and nutrient dynamics of TMF vary with degree of disturbance, as well as with elevation. The development of similar studies in other parts of the region (Afromontane tropical forests) is encouraged.

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