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Effect of community functional trait composition
on soil organic carbon dynamics between
Gilbertiodendron dewevrei monodominant forests
and *Scorodophloeus zenkeri* mixed forests in the
Central Congo basin

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"Je pense, je crois, je suis sûr, j'affirme que les forestiers devraient diriger le monde.

Pourquoi ?

Parce que, le forestier est, à l'instar des Indiens de l'Amazonie, celui qui, avant de se décider, jauge les conséquences de son choix pour les différentes générations à venir. On ne plante pas un arbre comme on fabrique un gouvernement, fût-il fédéral.

Les forestiers devraient conduire la terre, comme le dit Edgard Morin. Ils savent que les milliers de cernes du *Pinus aristata*, cet arbre chétif des Montagnes Rocheuses, peuvent lui dire plusieurs siècles d'histoire. Ils savent qu'une vie humaine n'est que poussière du temps face aux deux milles ans du gigantesque séquoia. Le forestier révère l'infinie majesté du temps."

Frédéric Lints, Louvain, 1993.

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Summary

As the second-largest continuous area of rainforest in the world, the Central African forest significantly affects global carbon (C) cycling and climate. Despite the substantial contribution of soils to C storage in African tropical forests, most studies focused on the living aboveground biomass. The drivers behind the variability in belowground C dynamics remain poorly studied. In tropical forests, little is known about the impact of vegetation on soil organic C (SOC) sequestration, more specifically under similar ecological conditions. Therefore, regional and global estimates of the rates of SOC gain and loss, as well as the size and permanence of the SOC stocks are still highly uncertain.

In the Congo basin, *Gilbertiodendron dewevrei* frequently occurs as large patches of monodominant forests (MOF) located next to higher diverse *Scorodophloeus zenkeri* forests (mixed forests, MIF). Although a series of functional traits, including leaf litter characteristics, have been shown to control monodominance in those systems, their role in regulating SOC dynamics remains largely unknown. In the present work, we examined how roots and foliar litter traits affected soil C dynamics (stocks and fluxes) under MIF and MOF located on highly weathered sandy soils in the Yoko reserve (DRC).

In addition to estimates of aboveground and soil (forest floor plus mineral soil down to 220 cm depth) C stocks, we measured soil respiration with and without forest floor contribution, aboveground foliar litterfall and fine roots production in topsoil (forest floor plus 0-10 cm layer) during a one-year period. Early leaf litter decomposition (≤ 6 months) of the 8 most abundant tree species and all their two-way combinations was assessed through a field incubation experiment.

We found similar total C stocks between forest types when cumulated over aboveground biomass, forest floor and mineral soil. By contrast, SOC stocks (forest floor plus mineral soil down to 220 cm) were 55 %

higher in MOF, and this difference was especially remarkable for the top 25 cm layer. Similar organic matter inputs were observed under both forest types but above- and belowground litter quality in MOF strongly differed by a set of traits related to organic matter recalcitrance; in particular leaf litter of *G. dewevrei* was located at the "conservative" end of the leaf economic spectrum (LES). Through our incubation experiment, we showed that the position of the litter along this LES strongly controlled the variation in leaf litter decay rates during the first 3 months of incubation suggesting contrasted decay rates between MIF and MOF. On an annual basis, soil respiration was 10% higher under MOF compared to MIF and forest floor removal significantly reduced soil respiration only in MIF, by *ca.* 18%. Based on a process-based conceptual model parameterized by environmental variables, MOF has been shown to favour the heterotrophic soil respiration through its twofold SOC accumulation.

By decreasing the decay rate of fresh organic matter and of soil organic matter, the low-quality litter of *G. dewevrei*, together with some other traits, increased C accumulation in soil under MOF compared to MIF leading to contrasted soil CO₂ efflux partitioning. However, the dominance of *G. dewevrei* did not appear to limit the aboveground C storage nor the net primary productivity (as inferred from similar above- and belowground litter production).

Our results highlight that reliable assessment of the global leaf and/or root economics spectrum should prove valuable in modelling SOC dynamics in tropical forests.

Abbreviations

AL _L	Annual leaf litterfall
AGB	Aboveground biomass
AGC	Aboveground carbon biomass
Al-o	Oxalate-extractable Al
AL _w	Annual fine woody debris litterfall
AR _A	Annual autotrophic soil respiration
AR _H	Annual heterotrophic soil respiration
AR _T	Annual total soil respiration
BA	Basal area
BA _w	Weighted basal area
CD _m	Chemical dissimilarity of the mixture
CEC	Cation exchange capacity
COP	Conference of the Parties
DBH	Diameter at 130 cm aboveground
DERM	Deviation from the expected relative remaining litter mass
DRC	Democratic Republic of Congo
DS _m	Decay stage of the mixture
EM	Ectomycorrhizal
Fe-o	Oxalate-extractable Fe
FF	Forest floor
FFC	Forest floor carbon
FR	Fine roots
FRP	Fine roots production
FRP _{FF}	Fine roots production in the forest floor
FRP _{MS}	Fine roots production in the 0-10 MS layer
<i>G. dewevrei</i>	Gilbertiodendron dewevrei (De Wild.) J.Léonard
GPP	Gross primary production

HFA	Home field advantage
ICP	Inductively coupled plasma
k	Maximum decomposition rate fitted by regression
k _{app}	Litter apparent decay rate
k _{inc}	Cumulated decay rates of MS from incubation experiment
LES	Leaf economics spectrum
MIF	Semi-deciduous <i>Scorodophloeus zenkeri</i> Harms mixed forests
MOF	Evergreen <i>Gilbertiodendron dewevrei</i> (De Wild.) J.Léonard monodominant forests
MRDI _m	Maximum relative decomposition index of the mixture
MS	Mineral soil
MSC	Mineral soil carbon
NEP	Net ecosystem production
O _F +O _H	Partly or strongly decomposed organic material
O _L	Non-decomposed fallen plant material
OM	Organic matter
PCA	Principal component analysis
R _A	Autotrophic soil respiration
R _H	Heterotrophic soil respiration
RM	Relative remaining litter mass
R _T	Measured daily total soil respiration
R _{WF}	Daily soil respiration without forest floor contribution
<i>S. zenkeri</i>	<i>Scorodophloeus zenkeri</i> Harms
SI	Shannon diversity index
SOC	Soil organic carbon (forest floor + mineral soil)
SVWC	Soil volumetric water content
TBCA	Total belowground C allocation
UNFCCC	United Nations Framework Convention on Climate Change
WSG	Wood specific gravity

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Chapter 1

General introduction

1.1 Tropical forests and climate change

The intensity of human impact on the planet earth and its functioning is increasing rapidly [Steffen et al., 2011; Malhi et al., 2014]. Through combustion of fossil fuel and land use changes (mainly deforestation), the concentration of atmospheric CO₂ (65% of greenhouse gases-GHG) strongly increased over the last few centuries. The atmospheric concentrations of CO₂ in 2011 was 40% greater compared to 1750 which strongly alters the energy balance at the Earth's surface [IPCC, 2013]. The current positive total radiative forcing leads to an uptake of energy by the climate system resulting in warming and changes in all components of the climate system (e.g., hydrosphere, atmosphere and biosphere). Most RCP (Representative Concentration Pathway) scenarios predict that global surface temperature change is likely to exceed 1.5°C but 2.0°C in worst scenarios (RCP6.0 and RCP8.5) [IPCC, 2013]. In term of precipitation, the contrasts both between wet and dry regions and between wet and dry seasons are expected to be reinforced. In addition to climate, human activity may affect other ecosystem regulating services such as biodiversity and nutrients and water cycles [Steffen, 2004].

Approximatively 56% of the anthropogenic emissions of CO₂ is absorbed by natural sinks, almost equally distributed between land and ocean [IPCC, 2013], while the remaining part stays in the atmosphere and contributes to the global warming. Through net growth via photosynthesis, forest ecosystems play a key role in the global C cycle by naturally storing and removing large amounts of atmospheric CO₂ [Canadell et al., 2007].

At the ecosystem scale, the net C balance (net ecosystem production, NEP) refers to the difference between the total amount of C fixed in the process of photosynthesis by plants (or gross primary production, GPP) and the losses through ecosystem respiration and disturbances (e.g. fires). Ecosystem respiration is the sum of autotrophic respiration due to the costs associated with growth and maintenance of plant

tissues and of heterotrophic respiration through organic matter decomposition by microbial activity. Positive NEP indicate that ecosystem acts as a CO₂ sink. Global terrestrial GPP is estimated to 122 Pg C year⁻¹ and is considered as the largest global carbon fluxes [Beer et al., 2010]. However, about 119 Pg C year⁻¹ are loss through respiration and additional disturbance processes leading to weakly positive and uncertain overall NEP [Luyssaert et al., 2007; Bonan, 2008]. In forest ecosystems, between 49 and 70% of GPP is released by autotrophic respiration in forest ecosystems [Luyssaert et al., 2007].

As shown by Figure 1.1, tropical forests are among the most productive terrestrial ecosystems, accounting for one-third of the global GPP, on only 12% of the area in the terrestrial biosphere [Bonan, 2008; Malhi, 2012]. Among those forests, tropical rainforests contribute the most to GPP due to the lack of a dormant period (winter or dry season). Indeed, the favourable high temperature and abundant precipitations in tropical rainforests ensure optimal conditions for C uptake via photosynthesis [Luyssaert et al., 2007; Beer et al., 2010]. Therefore, the role of tropical rainforests in climate change mitigation has received considerable scientific attention in the last decades [Lewis, 2006; Guariguata et al., 2008].

Global models often predicted an enhancement of the carbon cycling by climate warming through the kinetic sensitivity of photosynthesis and respiration to temperature [Luo, 2007]. Indeed, photosynthesis, plant growth, and primary production but also both autotrophic and heterotrophic respiration have been shown to be improved by increases in temperature and in atmospheric CO₂ concentrations [Lorenz and Lal, 2010]. However, experimental results are highly variable highlighting that NEP is also regulated by many processes other than photosynthesis and respiration kinetics, leading to complex responses to climate warming [Luo et al., 2009].

Currently, world forest C stock is estimated to 861 ± 66 Pg C equally distributed, in average, between biomass and soil [Pan et al., 2011]. Approximately 55% of the global forest C stocks is stored in tropical forests

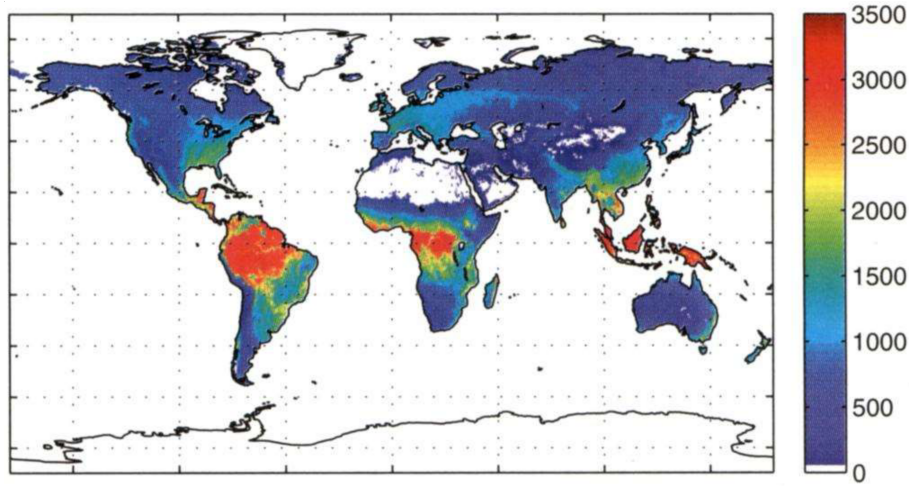


Figure 1.1 – The average gross primary productivity (GPP) in $\text{gC m}^{-2} \text{ year}^{-1}$ of the land surface, estimated from 1998–2005 (from Beer et al. [2010])

[Pan et al., 2011], with the Amazonian basin and the Congo basin being the two largest continuous blocks. However, these C stocks are currently at risk because of anthropogenic deforestation. From 2000–2007, the clearing of tropical forest and their conversion to different land use has resulted in emission of $0.45\text{--}1.7 \text{ Pg C year}^{-1}$ corresponding to 5–19% of global anthropogenic CO_2 emissions [Baccini et al., 2012; Harris et al., 2012]. However, NEP (C sinks) of tropical intact forest has been estimated to similar amounts over the same period ($0.55\text{--}1.49 \text{ Pg C year}^{-1}$). Therefore, the C budget reported in these forested ecosystems, source *vs.* sink of carbon, is still controversial [Clark, 2004]. Recently, Baccini et al. [2017] have shown that tropical forest could be a net C source through higher amount of C emitted than they can absorb. Through climate change and land-use changes, the key role of tropical forest in climate mitigation remains highly uncertain. This central question in the actual context need to be urgently addressed in the coming years.

Different schemes have been pursued to conserve tropical forests. One of the most significant developments arising from the Thirteenth Conference of the Parties (COP13) of the United Nations Framework Conven-

tion on Climate Change (UNFCCC) in 2007 was the REDD+ initiative. REDD+ is a set of policy approaches and positive incentives aiming at reducing emissions from deforestation and forest degradation in developing countries through conservation and sustainable management. More specifically, the REDD+ program aims to create a new financial incentive for developing countries by valorising the conservation and the enhancement of the existing forest C stocks through the C market. Recently, the parties to the UNFCCC reached a major milestone in 2015 during the COP21 through the Paris agreement. Indeed, the Paris agreement is the first binding universal agreement on the climate involving both developing and developed countries to implement and support the existing framework.

The implementation of the REDD+ mechanism needs to be supported by accurate additional information on C cycle components in tropical forests. Indeed, it is crucial to calibrate global C models with a good knowledge of the spatio-temporal variation of C stocks and its drivers in order to understand the future role of tropical forests in climate mitigation.

1.2 Belowground C sequestration in tropical forests

In average, tropical forests contain 242 Mg C ha^{-1} with more than 55% held by vegetation [Pan et al., 2011]. Due to easier accessibility, most studies focus on the aboveground biomass C pool (AGC) in tropical forests [Lewis et al., 2013; Chave et al., 2014]. Because of great variability (range from $57\text{--}375 \text{ Mg C ha}^{-1}$), global and regional estimates of AGC stocks remain highly uncertain and thus contribute to substantial error in estimates of C emissions from deforestation in the tropics. The large spatial variability in AGC storage has been shown to be mainly related to climate, soil and forest structure [Baraloto et al., 2011; Slik et al., 2010]. Through taller stature and higher wood density, African tropical rainforests exhibit larger AGC pool compared to Amazonian stands

[Lewis et al., 2013; Slik et al., 2010; Feldpausch et al., 2012; Lewis et al., 2004; Baker et al., 2004]. However, tropical forests in Central Africa remain largely underrepresented in pantropical forest biomass studies.

At the global scale, tropical forest soils account for one third of the terrestrial C storage [Jobbágy and Jackson, 2000]. Locally, the contribution of soil to C storage averages 36-60% under tropical forests [Don et al., 2011; Pan et al., 2011]. Most of the C stored in soil is not inert but in a continuous dynamic state of accumulation and decomposition [Janzen, 2004; Schrumpf et al., 2008]. Therefore, rapid climatic changes may alter soils from sinks to sources for atmospheric carbon [Davidson and Janssens, 2006]. Indeed, any net C loss from soil may potentially lead to an increase of atmospheric CO₂ concentrations whereas net OM accumulation in soil may contribute to reduce the amount of CO₂ in the atmosphere [Lal, 2004].

Despite the strong impacts that changes in SOC pool may have on the global carbon cycle, we are still lacking robust estimates of the spatial and temporal variability of SOC pools at local scale. Few studies have consistently addressed the drivers behind the variability in SOC sequestration in tropical forests while most of papers strongly focused on the aboveground part of C sequestration making rudimentary assumptions related to organic matter content and distribution in the soil profile for the belowground part. Because of the strong impact of land-use change and deforestation on soil C sequestration [Ramankutty et al., 2007], the quantification of the SOC stocks and its drivers is of major importance in the current context of global change.

In addition to mainly occur on nutrient poor and highly weathered soils [WRB, 2014], the tropical forests are not constrained by climatic factors such as temperature and precipitations. Therefore, the processes underlying soil C cycle in tropical forest likely differ than those in boreal and temperate forests. In the tropics, most available information about spatial variation in SOC stocks relate to regional/continental gradients, where climate, topography, soil texture, parental material, disturbance regime and land use (vegetation cover) affect SOC retention [Jobbágy

and Jackson, 2000; Silver et al., 2000; Saiz et al., 2012; Dieleman et al., 2013]. All these factors greatly interact to determine the physical, chemical and biological controls on organic matter in soil.

Locally, forest cover (e.g. forest structure and species composition) has been shown to explain substantially spatial variation in each component of soil C dynamics, through their impact on both biotic and abiotic conditions [Jobbágy and Jackson, 2000; Katayama et al., 2009]. However, all influencing factors strongly co-vary, which makes it difficult to separate the individual contribution of each factor. The impact of vegetation on SOC sequestration could be extracted from studies performed under controlled environmental conditions, more specifically under similar ecological conditions. However, contrary to boreal and temperate forests, such study cases in tropical forests are currently scarce [Schulp et al., 2008; Vesterdal et al., 2013; Dawud et al., 2016].

This study will investigate the drivers behind the influence of the forest cover on the SOC dynamics at local scale in Central African tropical forests. Relatively neglected in comparison to Amazon region and South-east Asia, forests in the Central Africa contributes one of the largest uncertainties about the role of tropical forest soils in climate mitigation [Ciais et al., 2011]. This is mainly because of a lack of resource for scientific research, insufficient infrastructure, limited logistical support and periodic political instability [Verbeeck et al., 2011; Malhi et al., 2013]. To reduce uncertainty in global estimates of SOC stocks and fluxes in tropical forest, more complete and higher quality information on spatio-temporal variation is required in this zone.

1.3 Forest type influence on soil C sequestration

C sequestration in forested ecosystem is defined by the rate of C gain and loss, the size of the C stocks and their permanence. More specifically, SOC sequestration is primarily controlled by the difference between C inputs and outputs in soil. Aboveground and belowground C inputs from vegetation and detritus C pools are the main C sources of OM in

soil while outputs are mainly driven by OM decomposition rate (Figure 1.2). Aboveground litter mainly includes woody part of the tree (e.g. twigs and bark), leaves, flowers and fruits. Belowground inputs derive from dead roots, mycorrhizial hyphae and root exudates. C losses from the soil originate from decomposition and mineralization processes of OM resulting in the heterotrophic component of soil respiration. It is important to note that the deadwood (coarse woody debris) pool was not considered in this study.

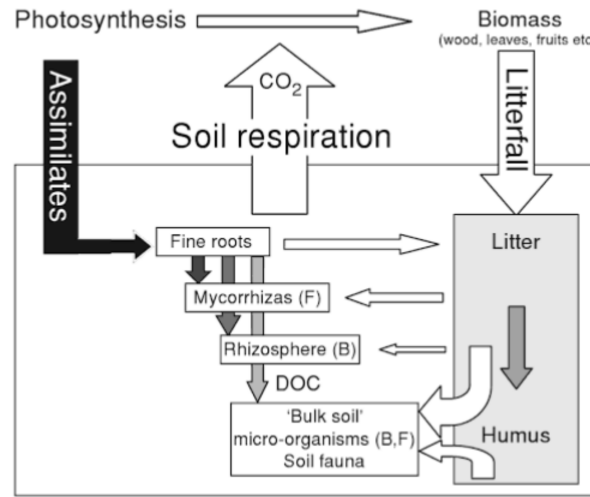


Figure 1.2 – Basic conceptual model of soil C dynamics (from Kutsch et al. [2009])

1.3.1 Species traits and SOC sequestration

Trees are characterised via a various set of functional traits defined as morphological, physiological and phenological features that represent ecological strategies and determine how plants respond to environmental factors, affect other trophic levels and influence ecosystem properties [Pérez-Harguindeguy et al., 2013]. Increasingly recognized as powerful indicators of plant form, function and performance [Violle et al., 2007; Díaz et al., 2016], functional traits are used to assess complex ecosystem processes. The functional traits provide a better mechanistic insight, in

contrast to taxonomic identity alone. Tree species identity impact on SOC sequestration is linked to functional traits that drive C assimilation, transfer and decomposition through the activity of autotrophs and heterotrophs, as well as through the modification of abiotic conditions [De Deyn et al., 2008].

The quantity and the quality of OM that plant return to soil has been shown to be strongly related to plant growth rate [Chapin, 2003; Lavorel et al., 2007]. Through greater photosynthetic capacity, tree species with higher growth rate are usually associated with higher net primary production and thus higher above- and belowground litter production. Compared to slow-growing species, aboveground and belowground plant organs of fast-growing species are characterised by shorter lifespan, lower dry matter content and lower C concentration [Aerts and Chapin, 2000].

Heterotrophic soil respiration and soil OM decomposition are determined by various influencing factors including litter quality, site-specific factors (such as soil properties) and the decomposer community [Coûteaux et al., 1995; Aerts, 1997; Hättenschwiler et al., 2005; Cornwell et al., 2008]. For a given site and climate, litter chemical and physical quality explains most of the reported variation in litter decomposition rate. Plant functional traits strongly influence the chemical and physical composition of OM inputs such as specific leaf area, nutrients (e.g. P, S, N) availability, lignin content and C:N:P:S stoichiometry. In tropical rainforests, OM decomposability is well predicted by all of these characteristics [Wieder et al., 2009]. Through longer residence time, recalcitrant litter forms may be beneficial for C sequestration at soil surface (or deeper through bioturbation) [Aerts, 1997; von Lützow et al., 2006; De Deyn et al., 2008].

Therefore, slow-growing species contribute to SOC pools through the input of litter with a set of traits related to recalcitrance (nutrient poor and high C concentration), whereas fast-growing species contribute via the input of significant amount of OM to soil. Bauters et al. [2017] have reported a strong influence of community composition on topsoil properties (e.g. pH, C and N concentrations) related to fresh and litter leaves functional traits in tropical forest plantations in the Congo basin.

In summary, functional traits that determine SOC sequestration operate through two different processes: (i) high primary productivity (large amount of C inputs) or (ii) reduced decay rate (low C output). It represents a new evidence of a trade-off between a set of traits promoting fast C acquisition and thus fast decomposition and another suite of traits which enhance the conservation of resources within well-protected tissues and slow decay [Grime et al., 1997; Wright et al., 2004; Diaz et al., 2004].

Indeed, at tree species level, there are fundamental physiological, evolutionary, and biogeochemical trade-offs expected to prevent the simultaneous maximization of the rate of C flow and the size and long-term permanence of C stocks [Diaz et al., 2009a]. These trade-offs are caused by allocation of limited resources to one purpose vs. another. Species that favour the most a specific C pool, such as aboveground biomass, are not necessarily the same as those that maximize another one, such as SOC. As an example, wood density represents a compromise between aboveground growth and mortality by insufficient physical strength and pest resistance [Wright et al., 2010].

Defined during the last few decades, the notion of an economics spectrum is frequently used to describe these fundamental trade-offs between functional life-history strategies among vascular plant [Givnish, 1986; Grime et al., 1997; Poorter and Bongers, 2006; Donovan et al., 2011]. The economics spectrum (including leaf, wood and root traits) is a pattern of correlation among plant functional traits which is strikingly consistent across and within species at both small and large scale [Osnas et al., 2013; Bardgett et al., 2014; Poorter et al., 2014; Reich, 2014; Díaz et al., 2016]. The study of trait spectra and trade-offs allows to explore the complex interplay of different functional strategies across species [Wright et al., 2007]. Several studies have reported the determinant role of the position of the species across the economics spectrum in explaining productivity or litter decomposition in tropical forests [Poorter and Bongers, 2006; Bakker et al., 2011; Finegan et al., 2015]. However, despite the crucial role of the functional traits, especially leaf traits, in explaining soil C dynamics, they remain yet poorly assessed in tropical rainforests.

1.3.2 Community-level species composition and SOC sequestration

Increasing tree species diversity increases the probability of including species with different life-story strategies and thus promoting greater variety of complementary functional traits which provide to species the opportunities to efficiently use the available resources (light, water, or nutrients), in agreement with the "niche complementary hypothesis" [Tilman et al., 1997; Diaz et al., 2009b]. Therefore, higher tree species diversity may be needed to maximize multiple ecosystem C pools at the same time [Nadrowski et al., 2010; Hulvey et al., 2013]. In addition, "selection effects hypothesis" suggests that forest ecosystems with a larger sample of species pool are also more likely to include high functioning species which will contribute strongly to ecosystem processes [Loreau and Hector, 2001]. Several studies have well documented positive effects of species diversity on SOC sequestration, microbial communities diversity, aboveground C storage and productivity in tropical forests [Gamfeldt et al., 2013; Cavanaugh et al., 2014; Poorter et al., 2015; Forrester and Bauhus, 2016; Mensah et al., 2016].

However, species diversity effects have also been reported to be weak or not significant [Sullivan et al., 2017]. Evidence is growing that forest C sequestration depends not only on species richness, but also on species identity, relative abundance and spatial arrangement [Peh et al., 2012; Scheibe et al., 2015; Dawud et al., 2016]. The "mass ratio hypothesis" postulates that the combined effects of functional traits of individual species at the community level are determined by their relative abundance resulting in strong influence of the most dominant values of tree functional traits on processes variability [Grime, 1998; Diaz et al., 2009a;b]. This hypothesis assumes that variations in forest function are determined by the presence or absence of highly performant tree species that can promote particular component of forest C sequestration [Finegan et al., 2015]. De Deyn et al. [2008] suggest that dominance of slow-growing species producing well-defended leaves and thus poor litter

quality strongly lead to reduce soil C losses through decomposition and thus enhance SOC storage.

In contrast to temperate and boreal forests, tropical rainforests are well known to exhibit the most species-rich plant communities. Sullivan et al. [2017] have reported forests with up to 300 tree species per ha. Nevertheless, primary tropical forests dominated by one or only few species are not uncommon whatever the continent [Peh et al., 2011b; 2014; Kazmierczak et al., 2016]. More than 22 species from eight different families are known to form naturally almost pure stands [Peh et al., 2011a]. In Central Africa, such low-diversity forests are frequently dominated by *Gilbertiodendron dewevrei* (De Wild.) J.Léonard (MOF) [Hart, 1985]. So-called monodominant forests, where more than 60% of the canopy-level trees belong to the same species [Connell and Lowman, 1989], are often found adjacent to significantly more-diverse forests such as *Scorodophloeus zenkeri* Harms mixed forests (MIF) [Hart et al., 1989; Peh et al., 2011b; Kearsley et al., 2017]. As shown by Mankou et al. [2017], MIF and MOF belong to a strong floristic gradient in Central Africa determined by two species; *G. dewevrei* and *S. zenkeri* Harms. This classical monodominance is mainly explained by two theories: (i) a lack of exogenous disturbance and (ii) species-specific life-history traits [Hart et al., 1989; Peh et al., 2011a]. In particular, *G. dewevrei* exhibit a unique combination of traits, including low leaf litter decomposition, high seedling shade tolerance, large seed size, and defense against herbivory; those traits provide a strong competitive advantage and contribute to achieving monodominance [Hart et al., 1989; Torti et al., 2001].

This monodominant (MOF) *vs.* highly diverse forests (MIF) combination occurs on a variety of substrates [Hart et al., 1989; Nascimento and Proctor, 1997; Peh et al., 2011b]. Such pairwise comparison of forests with contrasted species composition on similar ecological conditions (climate and edaphic) represent ideal conditions to assess the influence of forest types and their functional compositions on soil C dynamics.

1.4 Objectives and outline of the thesis

The overall aim of this thesis is to improve the knowledge of soil C cycling in tropical rainforest in the central Congo basin and more specifically to gain insight into the impact of forest type and species composition through their functional traits on the main soil C stocks and fluxes.

To achieve this goal, we investigate the main C stocks and fluxes in two emblematic forest types of the Central Congo basin, in DR Congo: the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). Both widely distributed throughout the Central Congo basin, MIF and MOF cover extensive areas in the zone and frequently co-occur on similar ecological conditions [Hart et al., 1989; Peh et al., 2011b; Kearsley et al., 2017].

Three major objectives are defined for this thesis, each associated to one chapter:

1. To assess the influence of forest type on C storage pattern in two contrasted old-growth forest types in Congo basin;
2. To quantify the impact of the position along the leaf economics spectrum on leaf litter decomposition for 8 major tree species and to identify the drivers behind non-additivity effects in their mixtures under tropical rainforest in Congo basin; and
3. To assess the forest type effect on soil CO₂ efflux with and without forest floor contribution and the factors influencing the partitioning between the autotrophic *vs.* heterotrophic components through a process-based conceptual model in two old-growth forest types contrasted with regards to species composition.

This thesis consists of 5 chapters: the introduction (Chapter 1), 3 research chapters (Chapters 2-4) and the general discussion and conclusions (Chapter 5). Each chapter focuses on a particular component of the C dynamics in soil; SOC stocks (Chapter 2), litter decomposition (Chapter 3) and soil respiration (Chapter 4). In the **introduction**, we

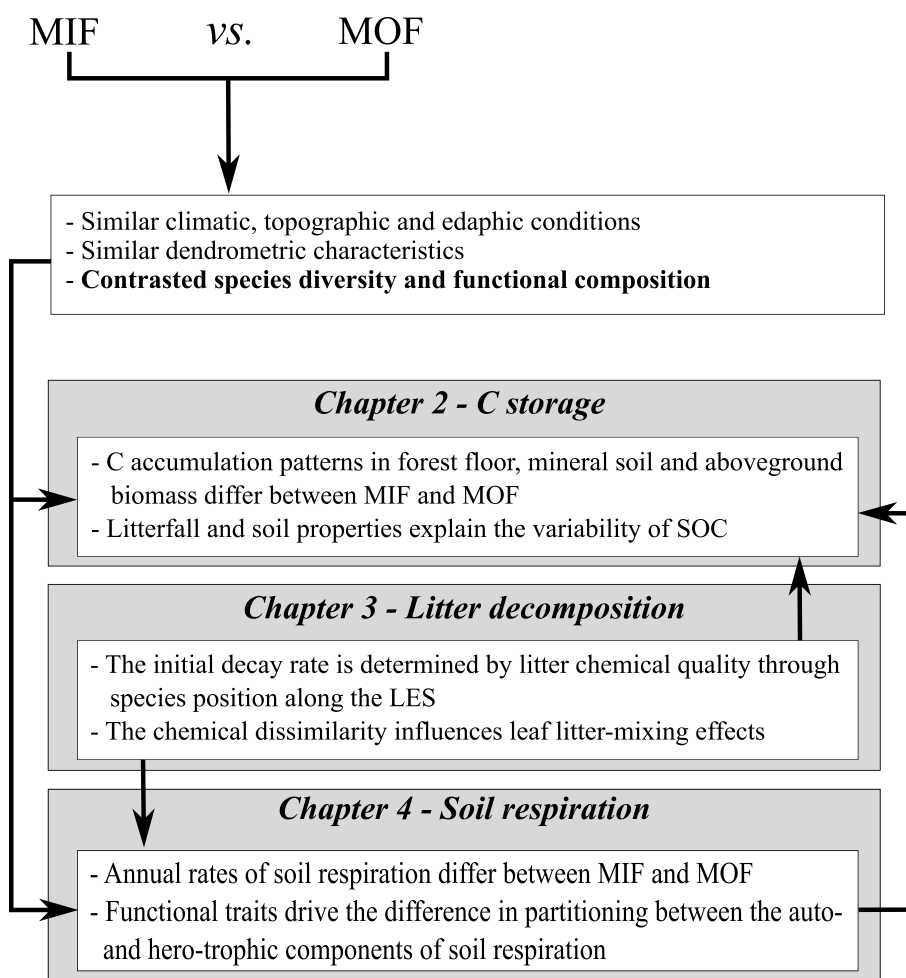


Figure 1.3 – Lay-out of the thesis, illustrating the hypotheses and the relation between the different chapters

sketched the grand challenges facing the planet Earth in the current context of global change. We pointed out the crucial role of forest and more specifically tropical forest and their soils in climate mitigation. Therefore, we identified several knowledge gaps and a need for studies of the impact of vegetation on SOC sequestration under controlled environmental conditions. In the study case of MIF and MOF on similar ecological conditions, we investigated different interrelated components of SOC cycle as described in the next chapters (Figure 1.3).

In **Chapter 2**, forest and soil characteristics are detailed for both MIF and MOF in the Yoko Reserve, near Kisangani, DR Congo. We assess soil organic C stocks (forest floor and mineral soil down to 220 cm depth) and aboveground C stocks. We then investigate the drivers related to litter inputs, stand characteristics and soil conditions which control SOC stocks and its accumulation in different soil layers (organic and mineral soil) under those contrasting forest types. In **Chapter 3**, we describe the litter quality of the eight most abundant species found under MIF and MOF. We investigate the relative effects of species identity, litter chemistry and incubation environment (MIF *vs.* MOF) on leaf litter decomposition over up to 6 months of incubation. We assess in what extent the position of species along the leaf economics spectrum is a good predictor of decay rate compared to individual traits. In addition we study the magnitude and direction of non-additive litter mixing effects on breakdown. In **Chapter 4**, we focus on the most important component of ecosystem respiration; the soil respiration. We investigate the seasonal and spatial variation in soil respiration with and without forest floor contribution. Through a process-based conceptual model that separates total soil respiration (R_T) into autotrophic (R_A) and heterotrophic (R_H) components parameterized by environmental variables collected in MIF and MOF, we assess the influence of forest types and species composition in soil respiration partitioning. In **Chapter 5**, in addition to suggest directions for further research, we provide a general overview and an integrated discussion of the key findings of this thesis.

Chapter 2

Contrasting patterns of carbon sequestration between *Gilbertiodendron dewevrei* monodominant forests and *Scorodophloeus zenkeri* mixed forests in the Central Congo basin *

*Adapted from Cassart, B., Angbonga Basia, A., Titeux, H., Andivia, E. and Ponette, Q., Contrasting patterns of carbon sequestration between *Gilbertiodendron dewevrei* monodominant forests and *Scorodophloeus zenkeri* mixed forests in the Central Congo basin, *Plant and Soil*, 414(1-2), 309-326, 10.1007/s11104-016-3130-8, 2017.

Abstract

Gilbertiodendron dewevrei (De Wild.) J.Léonard monodominant forests (MOF) and *Scorodophloeus zenkeri* Harms mixed forests (MIF) frequently co-occur on similar soil conditions in the Central Congo basin. Although tree species composition is known to impact C storage, the patterns of C sequestration between those contrasted forest types as well as the associated drivers remain unknown. Annual litterfall, as well as soil (forest floor and mineral soil down to 220 cm depth) organic C (SOC) and aboveground C (AGC) stocks were investigated in MIF and MOF located on highly weathered sandy soils in the Yoko Reserve (DRC). The annual leaf litterfall was similar under both forests but litterfall quality in MOF strongly differed by a set of traits related to organic matter recalcitrance. The SOC stock down to 220 cm was 55 % higher under MOF compared to MIF, and the differences between forests remained significant down to 100 cm. While the combined SOC and AGC stocks were similar in both forests, the SOC stocks accounted for ca 19 and 33 % of the total C stocks in MIF and MOF, respectively. Because of similar litterfall C inputs, we conclude that the greater SOC accumulation under *G. dewevrei* results from a limitation of the decomposition rate, in agreement with the traits of the corresponding leaf litter.

2.1 Introduction

More than 50% of terrestrial carbon (C) is stored in tropical forest ecosystems [Pan et al., 2011]. Tropical forests are among the most productive terrestrial ecosystems, accounting for one-third of global net primary productivity [Malhi, 2012]. The role of tropical forests in climate change mitigation has received considerable scientific attention in the last decades [Lewis, 2006; Guariguata et al., 2008] with increasing emphasis on the potential key role of soil [Lal, 2004].

Despite the contribution of soils (up to 1 m) to global C storage is estimated to 32 % in tropical forest [Pan et al., 2011], few studies have consistently addressed the drivers behind the variability in soil organic carbon (SOC) stocks. Most available information relate to regional/continental gradients, where climate, topography, soil texture, parental material, disturbance regime and forest type (vegetation cover) all co-vary [Jobbágy and Jackson, 2000; Silver et al., 2000; Saiz et al., 2012; Dieleman et al., 2013], which makes it difficult to separate the individual contribution of each factor. In that context, a better understanding of SOC variability would greatly benefit from studies performed under more controlled environmental conditions, using a factorial design. Under homogeneous conditions of climate and topography, this approach proves particularly relevant to extract the soil and/or vegetation signal. The knowledge gained could then be used to reduce uncertainty in regional and global estimates of C storage.

Using this approach, it has recently been reported that slight differences in soil properties could strongly impact SOC storage under similar forest types in the Central Congo basin, probably through change in allocation pattern [Doetterl et al., 2015b]. Contrary to boreal and temperate zones, the role of forest type / tree species composition in controlling SOC storage is still largely unknown in tropical forests. Most of the existing literature dealing with the effect of tree species composition on soil properties focused on how monodominance is achieved, while the impacts of tree species composition on SOC stocks received little attention

[Hart et al., 1989; Hart, 1995; Torti et al., 2001; Peh et al., 2011b]. Yet the results from other biomes show that tree species identity strongly impacts both the total SOC stock and its vertical distribution [Schulp et al., 2008; Vesterdal et al., 2013; Dawud et al., 2016].

Tree species identity impact on SOC sequestration is linked to functional traits that drive C assimilation, transfer and decomposition through the activity of autotrophs and heterotrophs, as well as through the modification of abiotic conditions [De Deyn et al., 2008]. While many forests from the temperate or boreal biomes are characterized by a relatively limited tree diversity, at least in Europe, tropical forests comprise a large range of tree species biodiversity, from ecosystems where nearly one single tree species dominates in the upper canopy layer, the so-called ‘monodominant forests’ [Connell and Lowman, 1989], to highly diverse forests with up to 300 tree species per ha [Gentry, 1988].

At tree species scale, physiological, evolutionary, and biogeochemical trade-offs are expected to prevent the simultaneous maximization of the rate of C acquisition and the size and long-term permanence of C stocks [Diaz et al., 2009a]. Species that favour the most a specific C pool, such as aboveground biomass (AGB), are not necessarily the same as those that maximize another one, such as SOC. Therefore, higher tree species diversity may be needed to maximize multiple ecosystem C pools at the same time [Nadrowski et al., 2010; Hulvey et al., 2013]. Increasing tree species diversity increases the probability of including species that have complementary functional traits for more efficient resource use, in agreement with the niche complementary hypothesis [Diaz et al., 2009a]. However ecosystem C storage does not only depend on tree species richness, but also on tree species identity [Dawud et al., 2016]. Following the mass ratio hypothesis, forest systems dominated by species with some unique combination of functional attributes can substantially promote a particular component of the C sequestration, i.e. dominance of slow-growing species producing well-defended leaves and thus poor litter quality strongly enhances SOC storage [De Deyn et al., 2008]. In the extreme case, the mass ratio hypothesis predicts that C storage would

even be maximized in a forest dominated by one single species combining the best performing traits in terms of C storage [Diaz et al., 2009b].

In addition to showing very contrasting ranges of tree species biodiversity, another major difference between tropical and other forest biomes relates to the C distribution pattern at the ecosystem level. Although most of the C in tropical forests is held in AGB [Lal, 2005; Pan et al., 2011], forest types induced differences in SOC:AGC ratio could strongly impact their respective long-term C sequestration capacity, as a result of contrasted SOC vs. AGC release following disturbances such as drought events, forest fires or deforestation [Fearnside, 2000; Frank et al., 2015].

Here we focus on two emblematic forest types of the Central Congo basin: the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). These two forest types cover extensive areas in the zone, where they frequently co-occur on similar ecological conditions on a wide variety of soils [Hart et al., 1989; Djuikouo et al., 2010; Kearsley et al., 2013]. In this context, it is particularly crucial to properly assess their impacts on SOC sequestration.

In this study, we assessed C stocks in MIF and MOF forest types under similar climate and edaphic conditions in a forest area of the Central Congo basin. More precisely, we aim at identifying the drivers related to litter inputs, stand characteristics and soil conditions which control SOC stocks and its accumulation in the different soil layers under those contrasting forest types. We hypothesized that:

1. differences in species composition between MIF and MOF forest types result in different C accumulation patterns in the forest floor and mineral soil and different SOC:AGC ratios, and that
2. differences in litterfall (quality and/or quantity) and soil properties induced by differences in stand characteristics (basal area and species composition) explain the variability of SOC accumulation at local scale within each forest type.

2.2 Materials and methods

2.2.1 Experimental site

This study was conducted in the Yoko reserve in the Tshopo province of the Democratic Republic of Congo (DRC). The reserve (N 00°19'12"; E 25°17'43") is located at about 28 km to the south of the city of Kisangani and covers an area of 6,975 ha.

The reserve is characterized by a main sandy plateau with an average elevation of 450 m dissected by a hydrographic network. According to the revised Köppen-Geiger classification, the regional climate is described as Af-type tropical rainforest climate [Peel et al., 2007]. Based on the meteorological data collected from the Yangambi station (located 100 km to the west of Kisangani) between 1961 and 2009, mean annual rainfall is 1780 (± 230) mm with two distinct rainy seasons (March-June and August-December), and a cumulated dry season length of ca 3 months (January-February and July) with monthly precipitation higher than 60 mm. The mean annual air temperature is 24.8 (± 0.5) °C with little seasonal variability. The dominant soil type is classified as Xanthic Ferralsol [Van Ranst et al., 2010; WRB, 2014] mostly composed of quartz sand, with low content of kaolinite clay and hydrated iron oxides. It is nutrient poor, deeply weathered and acidic.

The vegetation of the reserve is dominated by pristine moist semi-deciduous rainforest mixed with variable patches of moist evergreen rainforests. Few transition forests and slash-and-burn agriculture areas are found on the west side of the reserve along the road and on the east side along the Biaro River.

2.2.2 Plot location and characterization

A preliminary survey allowed to identify selected areas of the Reserve dominated either by MIF or MOF, in otherwise similar topographic and edaphic conditions.

Nine pedological pits were spread over those selected zones, and dug down to 220 cm to determine the main soil characteristics under both forest types; five pits were installed in MIF and four pits in MOF (Appendix 1). Soil samples were collected on each side of the pit and composited at 8 depths (0-10, 10-25, 25-50, 50-75, 75-100, 100-140, 140-180 and 180-220 cm). Bulk densities were determined per depth on one side, using Kopecky cylinders (100 cm³) after sieving at 2-mm and oven-drying at 105 °C. For each depth, subsamples were milled for total C and N analyses using the dry combustion method (Thermo Finnigan Flash EA 1112 elemental analyser). Soil texture, CEC and oxalate-extractable Fe (Fe-o) and Al (Al-o) were analysed on the 0-10, 75-100 and 180-220 cm layers. The coarse (0.2-2 mm) and fine (0.05-0.2 mm) sand fractions were separated by wet sieving following ultrasonication, while the silt and clay fractions were determined by a standard pipette method after dispersion with sodium hexametaphosphate. Soil CEC was determined by the ammonium acetate (leaching) at pH7. Fe-o and Al-o were extracted by the acid ammonium oxalate method [Carter, 1993], and determined by inductively coupled plasma (ICP) spectrometry. Acid ammonium oxalate removes both amorphous Fe- and Al-oxyhydroxides, poorly crystalline aluminosilicates and organically complexed Fe and Al from the soil; as those compounds have a high capacity to build covalent links with organic matter, this extraction can be used as an indicator of organic carbon stabilization capacity [Mikutta et al., 2006; von Lützow et al., 2006].

For both forest types, two plots of 0.83-ha (MIF) and 0.43-ha (MOF) each were then set up (Appendix 1). In all plots, all live trees with a diameter at breast height (DBH, diameter at 130 cm above ground or 50 cm above any buttresses) > 10 cm were measured and identified to species level, and all trees with DBH > 16 cm were mapped to determine local stand characteristics (see statistics section). Shannon Index and species richness have been calculated using a 0.22 ha reference area for all plots in MIF and MOF.

As shown in Table 2.1, the dendrometric characteristics, as well as the soil properties (except for the clay content in the 75-100 and 180-220 cm

Table 2.1 – Summary of forest and soil characteristics for the mixed (MIF) and monodominant (MOF) forests (averages $\pm$ standard deviations). Five most abundant species based on their basal area ratio (%). Fe-o and Al-o are respectively the oxalate-extractable Fe and Al of the soil layer. Different upper letters in a row indicate significant difference between forests ($p < 0.05$). All soil characteristics were determined in 5 (MIF) or 4 (MOF) pits

		MIF	MOF
Forest characteristics			
Stand density (tree.ha ⁻¹)		392 $\pm$ 13 ^a	405 $\pm$ 28 ^a
BA (m ² .ha ⁻¹)		31.4 $\pm$ 2.7 ^a	34.9 $\pm$ 6.5 ^a
Shannon index		3.12 $\pm$ 0.04 ^a	1.49 $\pm$ 0.01 ^b
Most abundant species		<i>S. zenkeri</i> (28.2%) <i>C. hankei</i> (7.0%) <i>J. seretii</i> (4.7%) <i>P. oxyphylla</i> (4.6%) <i>T. africana</i> (3.0%)	<i>G. dewevrei</i> (73.1%) <i>S. zenkeri</i> (7.8%) <i>P. oxyphylla</i> (6.0%) <i>C. griseiflora</i> (1.8%) <i>P. oleosa</i> (1.6%)
Soil characteristics			
pH H ₂ O	0-10 cm	4.2 $\pm$ 0.2 ^a	3.9 $\pm$ 0.3 ^a
	75-100 cm	4.6 $\pm$ 0.2 ^a	4.4 $\pm$ 0.1 ^a
	180-220 cm	4.8 $\pm$ 0.2 ^a	4.7 $\pm$ 0.1 ^a
Bulk density (g.cm ⁻³)	0-10 cm	1.17 $\pm$ 0.10 ^a	0.95 $\pm$ 0.24 ^a
	75-100 cm	1.40 $\pm$ 0.07 ^a	1.38 $\pm$ 0.09 ^a
	180-220 cm	1.58 $\pm$ 0.03 ^a	1.69 $\pm$ 0.05 ^a
Coarse Sand (0.2 mm-2 mm) (%)	0-10 cm	73.24 $\pm$ 4.18 ^a	75.53 $\pm$ 2.52 ^a
	75-100 cm	64.77 $\pm$ 4.85 ^a	69.81 $\pm$ 3.27 ^a
	180-220 cm	58.32 $\pm$ 3.75 ^a	63.88 $\pm$ 5.59 ^a
Fine Sand (50 μ m-0.2 mm) (%)	0-10 cm	13.42 $\pm$ 2.96 ^a	11.95 $\pm$ 1.03 ^a
	75-100 cm	15.92 $\pm$ 3.14 ^a	14.87 $\pm$ 2.45 ^a
	180-220 cm	20.72 $\pm$ 2.96 ^a	19.28 $\pm$ 5.54 ^a
Silt (2 μ m-50 μ m) (%)	0-10 cm	2.10 $\pm$ 0.47 ^a	2.70 $\pm$ 0.76 ^a
	75-100 cm	2.53 $\pm$ 0.36 ^a	2.53 $\pm$ 0.06 ^a
	180-220 cm	2.64 $\pm$ 0.53 ^a	3.08 $\pm$ 0.61 ^a
Clay (<2 μ m) (%)	0-10 cm	11.28 $\pm$ 1.33 ^a	9.85 $\pm$ 1.03 ^a
	75-100 cm	16.74 $\pm$ 1.84 ^a	12.79 $\pm$ 0.90 ^b
	180-220 cm	18.30 $\pm$ 1.55 ^a	13.80 $\pm$ 0.73 ^b
CEC (cmol _c .kg ⁻¹)	0-10 cm	3.1 $\pm$ 0.4 ^a	5.3 $\pm$ 2.0 ^b
	75-100 cm	2.0 $\pm$ 0.2 ^a	1.8 $\pm$ 0.1 ^a
	180-220 cm	1.7 $\pm$ 0.2 ^a	1.8 $\pm$ 0.1 ^a
Fe-o (mmol.kg ⁻¹)	0-10 cm	13.5 $\pm$ 2.6 ^a	15.2 $\pm$ 2.0 ^a
	75-100 cm	6.5 $\pm$ 0.8 ^a	8.1 $\pm$ 0.1 ^a
	180-220 cm	3.9 $\pm$ 0.5 ^a	3.9 $\pm$ 0.1 ^a
Al-o (mmol.kg ⁻¹)	0-10 cm	9.5 $\pm$ 1.6 ^a	12.4 $\pm$ 4.8 ^a
	75-100 cm	15.7 $\pm$ 0.8 ^a	13.7 $\pm$ 2.5 ^a
	180-220 cm	15.4 $\pm$ 1.7 ^a	13.6 $\pm$ 1.3 ^a

layers, and CEC in the 0-10 cm layer) were not significantly different between the two forest types. By contrast, species diversity quantified by the Shannon Diversity Index was much higher in MIF compared to MOF. In addition, while *S. zenkeri* accounted for 28.2% of the total BA in MIF, the contribution of *G. dewevrei* to total BA accounted for 73.1% in MOF allowing this forest to be classified as monodominant [Connell and Lowman, 1989]. Finally, tree species richness was higher in MIF (73 species) compared to MOF (51 species), while 42 species were shared between both forest types (Appendix 2).

2.2.3 Litterfall, forest floor and soil collection

Within each plot, 12 x 12 m square subplots were set up in a systematic way, resulting in a total of 72 and 32 subplots in the MIF and MOF respectively (Appendix 1).

Circular litter traps (1.3 m high and 1 m²) were installed in the center of each subplot and litterfall was collected monthly from May 2012 to April 2013. Coarse woody debris with a diameter > 1 cm were discarded and the remaining was sorted into two fractions (leaves and fine woody debris). All litterfall components were dried at 70°C during 48-h and weighed. Annual litterfall was calculated by summing up the monthly C inputs. C and N analyses by the dry combustion method (Thermo Finnigan Flash EA 1112 elemental analyser) were performed on composite litterfall samples of each litterfall fractions pooled over three months (May to July, Aug. to Oct., Nov. to Jan. and Feb. to April). In order to further characterize the leaf litterfall chemistry, Ca, K, Mg, Mn, P, S and Si concentrations were determined by ICP spectrometry after total acid digestion in a microwave system (Milestone UltraWAVE, Germany) for a random subset of subplots for the Nov. to Jan. period (22 and 20 in MIF and MOF, respectively); this particular period was selected to avoid any over-representation of deciduous tree species as would otherwise possibly occur in the dry season, while still ensuring the proper representativeness of the dominant tree species.

Forest floor (FF) was sampled in two randomly selected points per subplot next to the litterfall traps, using a 20 x 20 cm metal frame (Appendix 1). For each sample, the litter component (O_L) and the decomposed organic matter (O_H+O_F) were separated. Briefly, O_L was described as non-decomposed fallen plant material and O_H+O_F as partly or strongly decomposed organic material [van Delft et al., 2006]. Samples were then pooled per subplot for determination of oven-dry mass (70 °C during 48-h), and grinded for C and N analyses.

Mineral soil (MS) samples were collected at four locations per subplot at five depth increments (0–10, 10–25, 25–50, 50–75 and 75–100 cm), using an Edelman auger sand-type (Appendix 1). No coarse fragments were found in mineral soil samples; similarly, we did not detect any charcoal presence. Samples were then pooled into one sample per depth and subplot, air-dried, sieved at 2-mm and milled for C and N analyses. Bulk densities were determined at one location per depth and per subplot, using Kopecky cylinders (100 cm³) after sieving at 2-mm and oven-drying at 105 °C. Because forest type was expected to mainly affect the upper soil layers, topsoil (0-25 cm) layers were sampled in each subplot while 25-50 and 50-100 cm layers were randomly sampled in 50 % and 25 % of the subplots, respectively. Soil pH was determined potentiometrically on the 0-10 cm MS samples in 0.01 M CaCl₂ (1:5 soil:solution ratio).

In addition, fine roots were randomly sampled in 10 locations from the upper 0-10 cm MS layer in each forest type in March 2013, using Kopecky cylinders (200 cm³). Roots were removed from the soil by wet sieving and separated into fine (< 2mm) and coarse roots using a vernier scale; based on colour and buoyancy, dead fine roots were discarded. Roots samples were oven-dried at 70 °C during 48-h and grinded for C and N analyses. For comparison with the leaf litterfall quality data, newly senescent leaves of the dominant tree species (ie *S. zenkeri* and *G. dewevrei* in MIF and MOF, respectively) were randomly collected from the ground around the plot, composited by species, grinded and analysed for C, N, Ca, K, Mg, Mn, P, S and Si concentrations using the same methods as for the leaf litterfall samples.

2.2.4 Carbon stocks

The FFC stock (Mg ha^{-1}) was calculated by multiplying C concentrations in the layer (O_L or O_F+O_H) ($\text{g } 100\text{g}^{-1}$) by the layer dry mass (g), and dividing this by the sampled surface (400 cm^2). The MS C stock (Mg ha^{-1}) was obtained as the product of C concentration in the layer ($\text{g } 100\text{g}^{-1}$) by layer thickness (cm) and by layer bulk density (g cm^{-3}).

AGB (including stem and branches) of each tree in plots was calculated using Chave et al. [2014] equations based on total tree height, DBH and wood specific gravity (WSG). Tree height was estimated from local specific height-DBH regression models (three-parameters exponential) developed for a subset of twenty species accounting for 72 and 95 % of total basal area (BA) in the MIF and MOF, respectively (H:DBH allometry and species list including their relative BA are available in Appendices 3, 4, 5 and 6). A minimum of two trees per each 10 cm diameter class were selected throughout the corresponding tree species diameter distribution obtained from the dendrometric inventory. Tree heights were measured using a Vertex III hypsometer (Haglöf, Sweden). According to Bénédet et al. [2015], species were classified into three adult stature groups: "small", "medium" and "large" in terms of height. Based on this classification, one height-DBH model was performed per group to further estimate height for species non-sampled in this study context. WSG was determined for the same trees on two wood cores using a 3D X-ray scanner with $50\text{-}\mu\text{m}$ resolution [de Ridder et al., 2011]. For non-measured species, wood densities were extracted from the DRYAD database [Chave et al., 2009; Zanne et al., 2009] or estimated by genus-averages when species information was lacking. Cumulated AGB was calculated as the sum of the AGB of all trees using a 0.22 ha reference area for all plots [Chave et al., 2004], and aboveground carbon (AGC) stock was derived assuming that 49 % of biomass is made of C [IPCC, 2006].

2.2.5 Statistics

To test for differences in C stocks, stand characteristics, litterfall and soil properties between forest types, we applied mixed-effect models with forest type as a fixed effect term and subplot nested within plot as random effect terms for the different response variables.

A principal component analysis (PCA) was performed with the 11 foliar litterfall traits (Ca, K, Mg, Mn, P, S, Si concentrations and CN, CP, CS, NP ratios), using subplots ($n = 42$) as data points to explore the relationships among variables of litter quality and quantify the resulting difference of litter quality between forests, the senescent leaves of the dominant tree species of each forest ($n = 2$) were included as supplementary individuals.

In order to explore the possible drivers behind the variability of the upper C stocks (O_L , O_F+O_H , 0-10 cm, 10-25 cm, and combination for those layers) within each forest type, we used simple linear regression between the C stocks at the subplot level and a set of explanatory variables, and tested for significance (t test). The possible drivers were classified into the four following categories: (i) litter quantity (C inputs as leaf litterfall), (ii) litter quality (CN, CP, CS, NP ratios and the two principal components extracted from the previous PCA), (iii) stand parameters (total basal area (BA), BA of the dominant tree species, BA ratio of the dominant tree species and BA based Shannon diversity index (SI)), and (iv) soil parameters (CN ratio and pH of the 0-10 cm MS layer). For the stand parameters, a 15-m fixed radius around the centre of each subplot was selected in order to maximise the significance of the relationships between SOC and stand parameters based on the optimization procedure described by Bréchet et al. [2011]. Descriptive statistics for the effect of all potential drivers on SOC stocks are available in Appendix 7.

Before performing statistical analyses, the normality of all variables was tested by skewness and kurtosis normality test. All statistical analyses were performed in R version 3.2.0.

Table 2.2 – Leaf litterfall traits in the mixed (MIF) and monodominant (MOF) forests (mean $\pm$ standard deviation). p-values refer to the forest type effect.

Litter traits	Forests		p-values
	MIF	MOF	
C (%)	48.82 $\pm$ 1.73	50.16 $\pm$ 1.42	0.11
N (%)	3.10 $\pm$ 0.36	2.06 $\pm$ 0.21	0.01
Ca (g.kg ⁻¹)	14.72 $\pm$ 5.93	6.94 $\pm$ 1.66	0.08
K (g.kg ⁻¹)	5.22 $\pm$ 2.03	3.01 $\pm$ 1.02	0.04
Mg (g.kg ⁻¹)	3.21 $\pm$ 0.80	1.74 $\pm$ 0.34	0.01
Mn (g.kg ⁻¹)	3.78 $\pm$ 1.33	0.21 $\pm$ 0.17	< 0.01
P (g.kg ⁻¹)	1.25 $\pm$ 0.36	0.53 $\pm$ 0.15	0.01
S (g.kg ⁻¹)	6.24 $\pm$ 2.47	2.30 $\pm$ 1.38	0.06
Si (g.kg ⁻¹)	15.83 $\pm$ 5.42	19.51 $\pm$ 4.93	0.3
CN ratio	15.94 $\pm$ 1.90	24.49 $\pm$ 2.58	< 0.01
CP ratio	421.89 $\pm$ 114.84	1025.37 $\pm$ 362.10	0.02
CS ratio	91.21 $\pm$ 37.30	270.12 $\pm$ 108.96	0.03
NP ratio	26.49 $\pm$ 7.03	41.72 $\pm$ 13.55	0.06

2.3 Results

2.3.1 Comparison of litterfall quality and quantity between forest types

With 4.39 $\pm$ 0.74 and 4.15 $\pm$ 0.58 Mg C ha⁻¹ y⁻¹ in MIF and MOF, respectively, total litterfall (including leaves and fine woody debris) did not significantly differ between forests. Leaves litterfall accounted for similar proportions in both forests, amounting to 63% and 66% of total litterfall in MIF and MOF, respectively.

The foliar litterfall in MIF and MOF exhibited strongly contrasting chemical characteristics leading to a clear distinction between both forests according to the PCA analysis (Table 2.2, Fig. 2.1). The first axis accounted for 69% of the variation in the data and was positively related to litter Ca, K, Mg, Mn, P and S concentrations and negatively related to the different ratios (Pearson correlation coefficients between the litter traits in MIF and MOF are available in Appendix 8). Despite lower yet

Table 2.3 – Carbon stocks estimates in Mg C ha⁻¹ for MIF and MOF in the Yoko reserve (mean±standard deviation). Different upper letters in a row indicate significant difference between forests ($p < 0.05$).

Components		MIF	MOF
AGC		299.50±58.81 ^a	238.10±83.92 ^a
FF C stocks	O _L	0.90±0.33 ^a	0.80±0.22 ^a
	O _F + O _H	1.28±0.55 ^a	5.35±1.39 ^b
MS C stocks	0-10 cm	9.15±1.99 ^a	19.13±6.15 ^b
	10-25 cm	9.92±1.94 ^a	16.81±6.68 ^b
	25-50 cm	10.65±1.86 ^a	16.25±2.19 ^b
	50-75 cm	8.78±1.88 ^a	12.42±1.75 ^b
	75-100 cm	7.89±1.03 ^a	10.21±1.88 ^b
	100-140 cm	8.92±0.34 ^a	10.68±1.21 ^a
	140-180 cm	8.47±0.51 ^a	9.77±1.62 ^a
	180-220 cm	6.87±0.61 ^a	8.21±0.87 ^a
Total		372.33±60.97 ^a	350.73±83.66 ^a

significant contrast between forest types, foliar litter Si concentration determined the second axis, which explained 10.1% of the variation. Foliar litterfall in MIF were characterized by higher Ca, K, Mg, Mn, P and S concentrations and lower CN, CP, CS and NP ratios compared to MOF. The leaf litter traits of the dominant tree species *S. zenkeri* and *G. dewevrei* (Appendix 9) falls within the 90% confidence envelope delimiting the MIF and MOF forests, respectively (Fig. 2.1b). Within each forest type, the scattering of the data points along the two first PCA axes is large, suggesting a large range of leaf litter characteristics.

2.3.2 Comparison of carbon stocks between forest types

With 299.50 and 238.10 Mg C ha⁻¹ in the MIF and MOF respectively, the total AGC stock did not significantly differ between forests (Fig. 2.2, Table 2.3). The SOC stock cumulated over the FF and 0-220 cm MS accounted for 24 and 46 % of this quantity in MIF and MOF, respectively. When added to the corresponding AGC, it brought the total C

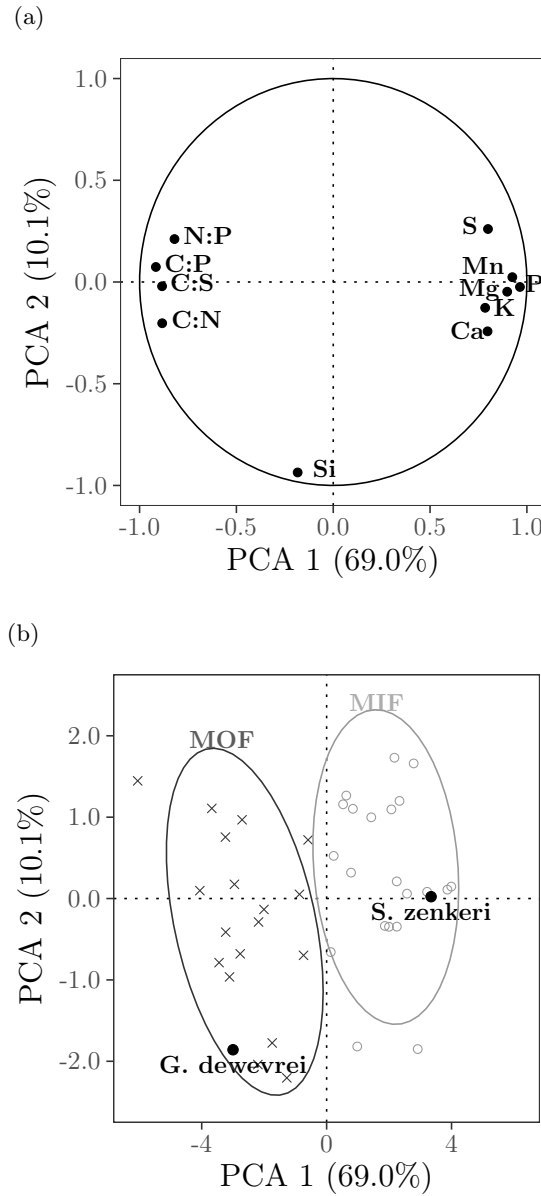


Figure 2.1 – Principal component analysis of 11 leaf litter traits from 22 and 20 litter traps in MIF (O) and MOF (X), respectively. Projection of a) variables and b) litter traps on the first two axes. Leaf litterfall of the dominant tree species was not included in the analysis but was plotted in the figure as supplementary individuals. Ellipses represent 90% confidence limits. Percentages in parentheses indicate the amount of variability each principal component accounts for in the data set.

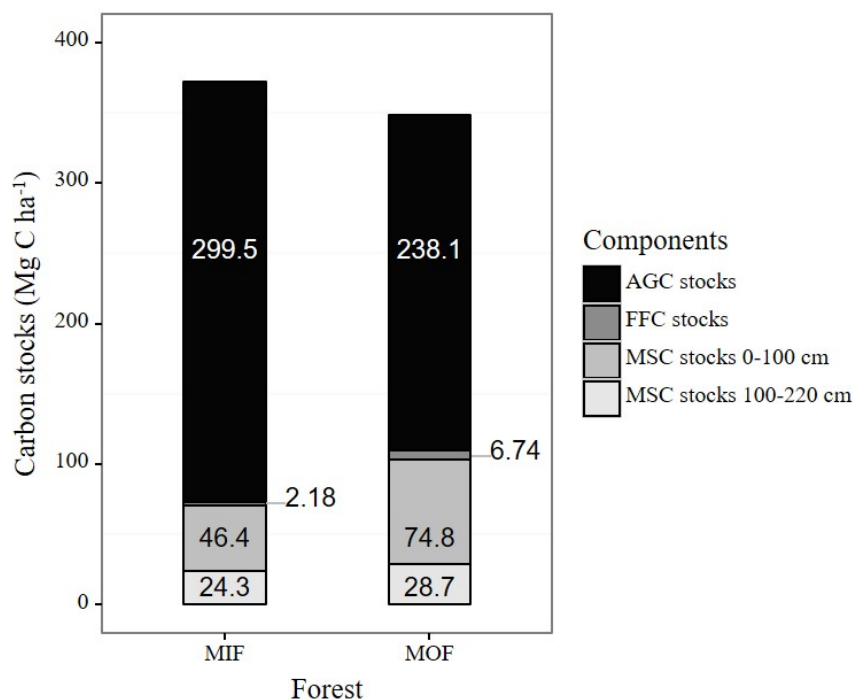


Figure 2.2 – Organic carbon stocks in the mineral soil (MSC; 0-100 and 100-220 cm layers), forest floor (FFC) and aboveground carbon biomass (AGC), in the mixed (MIF) and monodominant (MOF) forests.

stock of the ecosystem to similar level of 372.33 and 350.73 Mg C ha⁻¹, respectively.

The SOC stock in the FF plus the MS layer down to 1 m depth was significantly greater in the MOF (80.97 Mg C ha⁻¹) than in the MIF (48.57 Mg C ha⁻¹) (Table 2.3). The difference in C stored in the FF between forests was due to a fourfold C accumulation in the O_F+O_H layers under MOF (5.35 Mg C ha⁻¹) compared to MIF (1.28 Mg C ha⁻¹); by contrast, the C stocks in the O_L layer did not differ significantly between the two forest types. Significant differences in SOC stock between both forest types were observed for each MS layer down to 1 m depth, although the difference tended to decrease with depth. The first 25 cm of MS explained half of the difference in SOC stock between forest types down

to 1 m depth, while more than 75 % of the difference was accounted for by the first 50 cm of the MS (Fig. 2.3c). On the other hand, FF only accounted for about 10 % of the difference in total SOC stock down to 1 m depth between MIF and MOF. The MSC stored between 100 and 220 cm amounted to 24.26 and 28.66 Mg C ha⁻¹ on average in MIF and MOF respectively, and did not significantly differ between the two forest types. It represented 52 and 37 % of the C stored within the first meter of the MS, for the MIF and MOF, respectively.

The pattern of bulk density and MSC concentration with depth was similar in both forest types, showing a gradual increase and decrease, respectively (Fig. 2.3a and 2.3b). MSC concentrations were significantly higher in the MOF compared to the MIF down to 120 cm depth, with a MSC concentration in the 0-10 cm layer twice higher (0.81 % C and 1.58 % C in MIF and MOF, respectively); however this difference between forest types strongly decreased with depth. The C concentration in the deepest investigated layer (180-220 cm) was very low for both forests (0.11-0.12 % of C). BD in the top 1-m of the MS was slightly but significantly higher under MOF compared to MIF (mean difference around 0.07 g.cm⁻³). Below 1-m depth, bulk density stabilized at around 1.58 in MIF and 1.65 g.cm⁻³ in MOF.

2.3.3 Variability of SOC (FF and top MS) stocks within the two forest types

The adjusted R² of the linear regression between the C stocks for individual or selected combinations of upper soil layers and potential explanatory variables are presented in Table 2.4, together with the sign of the relationships. With the exception of the soil pH, the range of variation of all explanatory variables was large within each forest (Appendix 7).

The effects of litterfall parameters were mostly restricted to the OL horizon, and their contribution in explaining the variability of C stocks within a given forest type was quite limited in most cases. The O_L C storage was positively related to the annual leaf C litterfall and to the leaf lit-

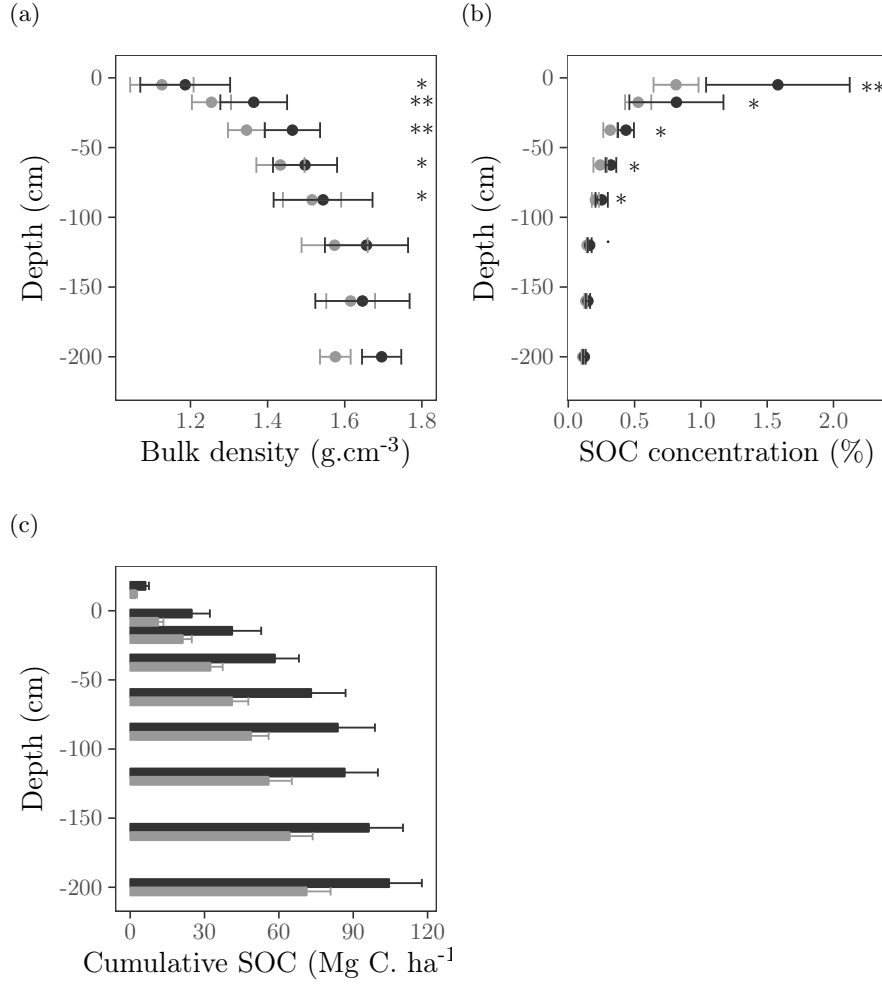


Figure 2.3 – Mean bulk densities (a), mean soil carbon concentrations (b), cumulative mean forest floor and mineral soil carbon stocks (c) as a function of depth in subplots and pits (down to 100 cm depth) and pits (from 100 cm down to 220 cm depth) in the mixed (grey) and monodominant (black) forests in the Yoko reserve. Error bars indicate standard errors. ·, *, ** denote respectively significant difference between forests at $p < 0.10$, $p < 0.05$ and $p < 0.01$.

Table 2.4 – Coefficient of determination (R^2) and sign of the slope for linear regression models ($Y = a + bX$) relating organic C stocks of upper soil layers (Y, Mg C ha⁻¹) to potential explanatory variables (X) within the mixed (MIF) or monodominant (MOF) forest. FF: forest floor, MS: mineral soil. *, **, *** denote a significant regression model at $p \leq 0.10$, $p \leq 0.05$ and $p \leq 0.01$. When the slope of the regression model is significantly different from 0, ↗ and ↘ denote respectively a significant positive and negative value. Dominant tree species are *S. zenkeri* and *G. dewevrei* in MIF and MOF respectively. The descriptive statistics for all potential explanatory variables within each forest type are reported in Appendix 7 while the coefficients of the linear regression models are given in Appendix 10

Variables	Forest	FF				MS				FF + MS	
		O _L		O _H +O _F		0-10 cm		10-25 cm		O _L +O _F +O _H + 0-25 cm	
Litter quantity											
C inputs as foliar litterfall (Mg C year ⁻¹ ha ⁻¹)	MIF	0.05**	↗	0.00		0.03		0.02		0.02	
	MOF	0.02		0.00		0.00		0.00		0.00	
Litter quality											
CN ratio	MIF	0.00		0.00		0.00		0.00		0.00	
	MOF	0.29**	↗	0.03		0.00		0.00		0.00	
CP ratio	MIF	0.01		0.00		0.01		0.00		0.00	
	MOF	0.00		0.00		0.02		0.00		0.00	
CS ratio	MIF	0.14*	↗	0.00		0.03		0.00		0.00	
	MOF	0.03		0.00		0.00		0.00		0.00	
NP ratio	MIF	0.02		0.00		0.00		0.00		0.00	
	MOF	0.00		0.00		0.00		0.00		0.00	
PCA 1	MIF	0.00		0.02		0.01		0.00		0.00	
	MOF	0.04		0.00		0.00		0.00		0.00	
PCA 2	MIF	0.15*	↘	0.02		0.00		0.10*	↘	0.05	
	MOF	0.02		0.00		0.00		0.00		0.00	
Stand parameters											
Total BA (m ² ha ⁻¹)	MIF	0.00		0.00		0.07**	↗	0.05**	↗	0.06**	↗
	MOF	0.00		0.00		0.06		0.00		0.01	
Dominant tree species BA ratio	MIF	0.00		0.00		0.10***	↗	0.07**	↗	0.12***	↗
	MOF	0.00		0.00		0.09*	↗	0.00		0.01	
Dominant tree species BA (m ² ha ⁻¹)	MIF	0.00		0.00		0.02		0.00		0.02	
	MOF	0.00		0.07*	↗	0.07*	↗	0.00		0.00	
Shannon diversity index (SI)	MIF	0.04		0.03		0.10***	↘	0.05**	↘	0.10***	↘
	MOF	0.00		0.00		0.03		0.00		0.00	
Soil parameters											
pH CaCl ₂ 0-10 cm	MIF	0.04*	↘	0.03		0.47***	↘	0.15***	↘	0.38***	↘
	MOF	0.02		0.05		0.76***	↘	0.14***	↘	0.55***	↘
CN ratio 0-10 cm	MIF	0.14***	↗	0.00		0.48***	↗	0.17***	↗	0.40***	↗
	MOF	0.00		0.00		0.05		0.03		0.04	

terfall CS ratio in MIF ($p = 0.04$, $R^2=0.05$ and $p = 0.08$, $R^2=0.14$, respectively), as well as to the CN ratio in MOF ($p = 0.03$, $R^2=0.29$). The principal components from axis 2, which were negatively related to foliar litterfall Si concentration (Fig. 2.1), were negatively related to C storage in the OL and in the 10-25 cm layer for MIF only.

The effects of stand characteristics were limited to the upper MS, and their overall explanatory power was also limited. There was a significant positive relationship between MSC storage, and both total BA and *S. zenkeri* BA ratio under MIF. In MOF, the 0-10 cm MSC stocks significantly increased with an increase in *G. dewevrei* BA (BA ratio: $p=0.08$, $R^2=0.09$; BA: $p=0.06$, $R^2=0.07$). Finally, SOC storage was negatively related to local stand diversity in MIF; however, strong relationships were observed between *S. zenkeri* relative or absolute BA and SI ($SI = 2.07 - 0.99 \cdot BA$ *S. zenkeri* ratio; $R^2 = 0.36$, $p < 10^{-5}$).

In general, the C stocks were much more strongly related to the investigated soil properties. For both forests, the C stored in the upper MS layers as well as in the cumulated FF + MS decreased as pH decreased (Table 2.4, Fig. 2.4a). In the MIF, the C stocks of all investigated layers, with the exception of the O_F+O_H layer, significantly increased as the 0-10 cm soil CN ratio increased (Fig. 2.4b); by contrast, no significant effect of the CN ratio was observed in the MOF. None of the soil parameters were related to either litterfall or stand characteristics (data not shown).

2.4 Discussion

2.4.1 Aboveground vs. belowground carbon stocks

While the 0-100 cm MSC stocks in MOF were almost similar to the average value reported by Batjes [2014] for Xanthic Ferralsols (82 Mg C ha⁻¹), the MSC stocks in MIF were about twice lower. When compared to the values reported for tropical deciduous and evergreen forests by Jobbágy and Jackson [2000], both forests had much lower MSC stocks

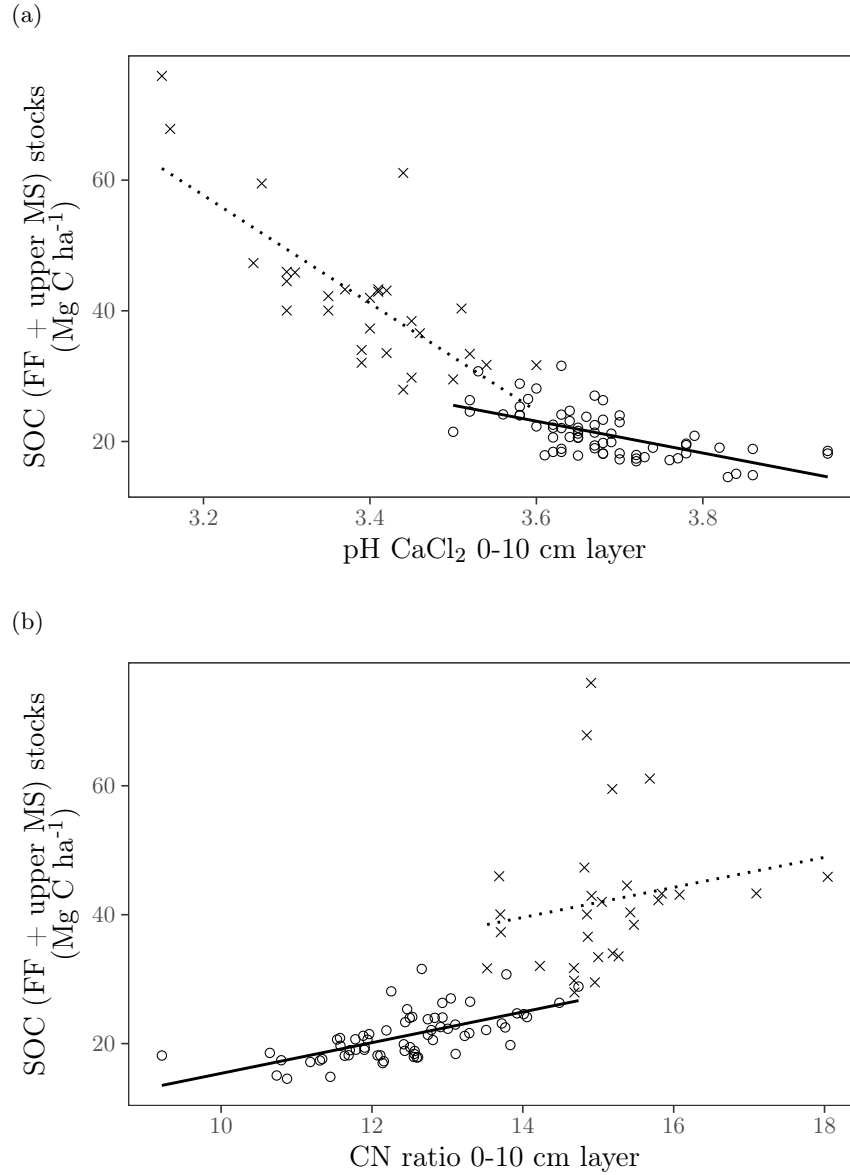


Figure 2.4 – Relationships between the pH CaCl_2 (a); C:N ratio (b) in the 0-10 cm layer and the upper soil organic carbon (forest floor + 0-25 cm layer) stocks in the mixed (MIF, (o)) and monodominant (MOF, (x)) forests, in the Yoko reserve. R^2 of fitted lines: (a) 0.38 ($p < 10^{-5}$) and 0.55 ($p < 10^{-5}$), (b) 0.41 ($p < 10^{-5}$) and 0.05 (NS) respectively, in MIF and MOF.

(from 2 to 4 times in the MOF and MIF, respectively). Such differences are not unexpected due to the large range of soil properties associated with tropical forests and Xanthic Ferralsols. The coarse sandy texture (>80 % sand fraction in the 0-100 cm depth, Table 2.1) of our soils is known to be quite unfavourable to carbon stabilization because of the low content of reactive surfaces [von Lützow et al., 2006].

The 0-100 cm layer contributed for 66 and 72 % to total MSC storage down to 220-cm depth in the MIF and MOF, respectively. Overall, these results are consistent with the contribution of 63 % reported by Batjes [2014], and support our observation of greater C accumulation in topsoil under MOF.

Estimated AGC stocks in this study (299.50 and 238.10 Mg C ha⁻¹ in MIF and MOF, respectively) are consistent with observed range (57-375 Mg C ha⁻¹) of AGC reported by Lewis et al. [2013] for tropical forests in Central Africa with a mean of 215 Mg C ha⁻¹; comparable estimates were also reported by Nasi et al. [2009]. However, AGC reported for *G. dewevrei* monodominant forests by Lewis et al. [2013] in DRC (Ituri district) and by Djuikouo et al. [2010] in Cameroon (Dja Reserve) are 25 % higher than those found in this study. By contrast, Kearsley et al. [2013] observed strongly lower AGC in mixed (160.5 Mg C ha⁻¹) and *G. dewevrei* monodominant forests (165.5 Mg C ha⁻¹) in Yangambi (100 km west of Kisangani), and attributed these low stocks to difference in diameter-height allometry. Although not measured in this study, below-ground biomass C stocks are expected to substantially contribute to total biomass C stocks. Assuming an average contribution of roots to AGC of 24% [Cairns et al., 1997; Mokany et al., 2006], C storage in coarse roots would amount to 71.9 and 57.1 Mg C ha⁻¹ in MIF and MOF, respectively. Nevertheless, root:shoot ratios and rooting depth remain highly uncertain [Waring and Powers, 2017]. Whereas strong interspecific variation in root architecture is expected [Townsend et al., 2008; Hallé et al., 1978] there is insufficient reliable data to adequately estimate root biomass in MIF and MOF, distinctly.

In both forests, aboveground vegetation held the biggest part of the C stocks. Indeed, AGC accounted for 81 ± 3 and 67 ± 9 % of the sum of all investigated carbon stocks (including AGC, FFC and MSC stocks down to 220 cm depth) in MIF and MOF, respectively, which is in agreement with the well-known latitudinal pattern in C storage partitioning between soil and vegetation components [Lal, 2005]. However, despite similar total C stocks among forests, our results clearly show a much greater SOC contribution under MOF compared to MIF. From a long-term C sequestration perspective, this forest type induced difference in C distribution could result in contrasting C release following disturbances such as drought events, forest fires or deforestation [Fearnside, 2000; Frank et al., 2015]. While current C monitoring projects for central African forests focus on aboveground pools [Lewis et al., 2013], our findings clearly show the importance of including reliable SOC estimates, in particular, by considering the strong impact of forest type on this key component of C sequestration capacity [Diaz et al., 2009a]. Doetterl et al. [2015a] already pointed out a similar shift in AGC:SOC ratios, but in that case for similar stand types growing under contrasting soil conditions.

2.4.2 Difference of SOC storage between forest types

For both forests, the contribution of FFC to SOC in the first meter was quite limited being less than 8 %. This was in strong contrast with the 0-25 cm topsoil layer that stored more than 40 % of the 0-100 cm, in agreement with values given for tropical old-growth forests [Jobbágy and Jackson, 2000].

Significant contrasts were observed in FFC storage between mixed and monodominant forests. Greater C accumulation in FF under *G. dewevrei* is consistent with other studies in Central Africa that already reported triple accumulation of FF dry mass in *G. dewevrei* forest in comparison to adjacent mixed forest [Torti et al., 2001; Peh et al., 2012]. Analogously, C stored in the MS (down to 220 cm depth) was 48 % greater in the MOF than in the MIF, and this difference was especially remarkable for

the top 25 cm layer. Contrary to numerous reports from temperate and boreal forests where tree species impacts are limited to the topsoil with a compensation between C accumulation in holorganic and upper MS in some cases [e.g. Augusto et al., 2003; Ngo et al., 2013; Vesterdal et al., 2013], this was by no means the case as MOF consistently showed a significantly greater C accumulation in the FF and MS down to 100 cm depth.

SOC stocks are primarily controlled by the difference between C inputs and outputs in soil. Aboveground and belowground litter production account for the major inputs of OM in soil while outputs are mainly driven by OM decomposition rate.

OM inputs through annual aboveground litterfall and fine roots production did not differ between forest types. Indeed, in one year, 2.71 ± 0.49 and 2.75 ± 0.44 Mg C ha⁻¹ of foliar litterfall fell on the ground in MIF and MOF, respectively (Appendix 7); this similarity in litterfall C inputs is in agreement with previous reports [Torti et al., 2001; Peh, 2009]. In addition, the fine root production in the FF and topsoil (0-10 cm) were comparable in both forests, amounting to 0.14 and 0.12 Mg.ha⁻¹.month⁻¹ in MIF and MOF, respectively (Cassart et al., unpublished results). Therefore, differences in SOC stocks between forests cannot be explained by OM inputs.

In given climate conditions, OM decomposition rate is driven by numerous interacting factors and processes, including (fresh) OM composition, geochemistry, physical protection / disconnection, living organisms, and soil microclimate [von Lützow et al., 2006; Schmidt et al., 2011].

All foliar litterfall traits analysed in this study differed significantly between MIF and MOF (Table 2.2). Larger Ca, K, Mg, Mn, P and S concentrations were observed in MIF, whereas higher Si concentrations as well as CN, CP, CS and NP ratios were found in MOF. Based on the large body of literature, those differences in litterfall chemistry are all expected to induce contrasting organic matter decomposition rates, especially in the first decomposition stages [Cornwell et al., 2008; Bakker et al., 2011]. Although it is difficult to point out specific traits involved

in the lower decomposition rate under MOF due to their correlations (Fig. 2.1a, Appendix 8), the higher CN and CP ratios are clear indications of lower N and P availability in MOF inducing lower C, N and P use efficiency of decomposers community [Enriquez et al., 1993; Zhang et al., 2008]; this is consistent with previous studies of Torti et al. [2001] and Peh et al. [2012]. Quite interestingly, the biggest relative differences in litter traits between forests were observed for Mn concentrations (3.78 and 0.21 g kg^{-1} in MIF and MOF, respectively), an element known to be involved in the late OM decomposition stages [Berg et al., 2007; Keiluweit et al., 2015]. Finally, *G. dewevrei* is known to produce amorphous silica, named phytoliths, in leaves and fruits [Runge and Runge, 1996]. Phytoliths are highly resistant to dissolution and may accumulate in the upper horizons of soils [Torn et al., 1997]. In addition, a high silica content in litter may reduce the decomposition rate by decreasing the digestibility and increasing the abrasiveness of plant residues [Hunt et al., 2008]. Although difference in foliar litterfall quality could lead to difference in topsoil carbon accumulation between MIF and MOF as a result of downward transport of soil C in the soil profile, it could hardly explain alone the sustained difference observed down to 1 m depth. Rather, this pattern suggests some parallelism between the root detritus and the foliar litterfall chemistries under both forests. This hypothesis is partly supported by the significantly higher CN ratio of the fine roots produced in MOF (35.82 ± 9.08 , $n=10$) compared to MIF (23.23 ± 4.60 , $n=10$).

Evergreen tree species are known to usually exhibit traits consistent with nutrient conservation strategies, i.e. lower nutrient content and specific leaf area but higher lignin content [Aerts and Chapin, 2000; Givnish, 2002]. This set of traits is related to a lower litter decomposition rate and thus likely to an enhancement of SOC storage. In the present case, however, the so-called semi-deciduous MIF [Lebrun and Gilbert, 1954] only contains a limited fraction 10-20% of deciduous tree species, and deciduousness of several of these species is still under debate [Couralet, 2010; Bénédet et al., 2015]. In addition, although classified as evergreen, *S. zenkeri* exhibits some leaf traits with characteristics associated with deciduous species (Appendix 9).

Although forest ecosystems with more species have a greater probability of including a larger functional trait diversity [Loreau et al., 2001; Diaz et al., 2009a], the range of leaf litter traits is surprisingly comparable in both forests (Fig. 2.1b). The two forests, however, occupy clearly distinct positions along the leaf litter characteristics spectrum, and this probably contributes to the overall limited impact of litter quality and stand parameters on C storage when considering each forest type separately (see next section). On the other hand, this pattern of leaf litter traits raises questions about the drivers of community assemblage in those two forests, as those appear to concentrate tree species with distinct leaf litter attributes; from that point of view, it would certainly be interesting to increase our knowledge about a larger range of functional traits. Although our study did not intend to separate between the effects of tree species diversity (tree species richness) vs. tree species identity, but simply aimed at comparing two forest types differing, among others, by tree species richness, our results clearly show the importance of tree species identity in determining the overall soil C sequestration capacity in tropical forests. Further insight would need to document a wider range of traits possibly involved in C storage [De Deyn et al., 2008] for a larger proportion of the tree species pool associated to each forest.

In the present case, geochemistry is not expected to explain the difference in C accumulation between forests (the correlations between the 0-10 and 10-25 cm SOC stock, and the clay or silt content in the 0-10 cm soil layer for MIF and MOF in the soil pits are available in Appendix 11). Although significant for some mineral horizons, the difference in clay content between forests remains quite limited (<5%; Table 2.1); in addition, the higher C concentrations in MOF are associated with lower clay content (Table 2.1, Fig. 2.3b), which is contrary to expectation [Feller and Beare, 1997]. On the other hand, oxalate-extractable Al and Fe are not significantly different between forests (Table 2.1).

Besides its possible implication in *G. dewevrei* monodominance [Torti and Coley, 1999; Peh et al., 2011a], the mutualistic association between roots and ectomycorrhizal (EM) fungi could increase SOC accumulation under MOF by at least two mechanisms [Langley et al., 2006]: it could

specifically slow down fine roots decomposition by ensheating the roots; it could also reduce OM decomposition as a whole by competitive interactions with the decomposer community. This latter mechanism is of particular relevance as it would further reduce the already limited P supply to the decomposer community, resulting from the combination of a very nutrient poor soil in the Yoko reserve (Table 2.1) and of the low P concentration of the leaf litterfall under MOF (Table 2.2).

The significantly higher bulk density observed in the upper soil layers under MOF despite higher SOC concentration (Fig. 2.3a and 2.3b) could indicate a lower mesofauna activity. This is in agreement with Torti et al. [2001] who observed five times less leaf-litter arthropods under a *G. dewevrei* forest in comparison to an adjacent mixed forest. Finally, thicker FF and greater soil OM content tend to increase water retention in sandy soil and bring inadequate aeration inducing a reduction of the activity of decomposers [Rawls et al., 2003; Nunan et al., 2003].

2.4.3 Variability of SOC (FF and top MS) stocks within forest types

Altogether, the litterfall (quantity and quality) and the stand characteristics appeared to have much more limited impacts on the variability of SOC stocks within each forest type, compared to the soil properties.

No strong patterns have been observed between litterfall characteristics (C inputs and litterfall quality) and C stocks within forest types except in the O_L . The limited impact of litterfall quantity on C storage despite a two-fold range in SOC stored in FF and 0-25 cm depth (21.25 vs. 42.09 Mg C ha⁻¹ in MIF and MOF, respectively) suggests that factors involved in OM decomposition would play a major role. While foliar litterfall quality explained difference of SOC between forest types, litter quality itself appears to be insufficient to drive the variability of litter accumulation within MIF and MOF. Because their effects are restricted to the O_L layer, the characteristics of the foliar litterfall (C inputs and litterfall quality including C:N ratio) within a forest type seem to have an

impact, yet limited, on the very first steps of the decomposition process. This is in strong contrast to the effects of the C:N ratio of the 0-10 cm MS layer, at least in the MIF (further discussed below).

For MOF, none of the studied stand parameters were related to C storage in the upper layers with the exception of a small significant positive effect of *G. dewevrei* BA (absolute and/or relative to total BA) on FF and/or 0-10 cm. This is in strong contrast to MIF, where upper soil C storage (MS layers and cumulated FF+MS layers) was significantly correlated to total BA, *S. zenkeri* BA ratio and SI. Increased total stand BA has often been reported to increase SOC accumulation in the FF under temperate forest as a result of increasing litterfall C inputs [Díaz-Pinés et al., 2011; Vesterdal et al., 2013]. The SI was inversely related to the proportion of *S. zenkeri* in the local BA in MIF ($SI = 2.07 - 0.99 \times S. zenkeri$ ratio; $R^2 = 0.36$, $p < 10^{-5}$), and this inverse relationship translates into opposite signs when those variables are correlated with the soil stocks (Table 2.4). As a result, one cannot conclude whether the decrease in C accumulation associated with the increase in the SI is a true diversity effect or a simple dilution effect. Note that a similar inverse relationship between SI and relative and/or absolute BA of *G. dewevrei* was also observed for MOF. Although we cannot conclude between the tree species identity vs. species diversity effect in the present case, it is important to point out that in the MIF, mean local BA proportion of *S. zenkeri* was about 26 % (Appendix 7); this means that any specific effect of *S. zenkeri* is potentially counteracted by a strong background of other tree species. This is in contrast with the MOF, where the mean local BA ratio of *G. dewevrei* is about 67 % (Appendix 7). In addition, *G. dewevrei* is characterized by an array of traits at the lower end of the decomposition gradient, while *S. zenkeri* stands in a more central position of the ‘decomposition spectrum’ (Fig. 2.1b).

The overall lack of consistency between the leaf traits impacts at the forest (i.e. between MIF and MOF) vs. local scales (i.e. within each forest type), as well as the limited correlation between the stand variables and C sequestration at the subplot level suggest that the species composition signal is too low compared to other drivers of C accumulation at those

local scales. Indeed, it is highly probable that disturbances such as large woody debris or tree uprooting play a significant role [dos Santos et al., 2016].

The CN ratio of the top (0-10 cm) MS was strongly and inversely related to SOC accumulation under the MIF, which suggests that N availability could be a factor limiting the decomposition process under this type of forest. However, the drivers behind this varying N availability remain unclear because there was apparently no relationship to litterfall CN ratio. Biological N fixation represents the major natural source of available N to those ecosystems [Galloway et al., 2004] and is mainly associated to trees from the Fabaceae family which comprise an important part of canopy trees in tropical forests [Crews, 1999]. In contrast to the MIF, there was no significant correlation between the soil CN ratio and SOC storage in MOF. The overall higher soil CN ratio under MOF compared to MIF (Appendix 7) is consistent with the higher CN ratio of the corresponding leaf litter (Table 2.2); in addition, although *G. dewevrei* is a member of the Fabaceae family, it has not been reported to nodulate with *Rhizobium* in old-growth evergreen forest [Doumenge, 2012]. So, while N limitation cannot be ruled out, other factors could therefore have played a major role. Among those, P has been hypothesized to be limiting in many tropical forest soils [Hedin et al., 2003]. The already soil-limited P could be further enhanced by plant-mediated process driven by some traits associated to *G. Dewevrei*. The leaf litter of *G. Dewevrei* is characterized by a remarkably low P nutrient concentrations (0.56 g kg^{-1} and 1.52 for *G. dewevrei* and *S. zenkeri*, respectively; Appendix 9); on the other hand, as explained above, the EM association could further reduce P availability to the decomposers community [Langley et al., 2006].

Among all tested variables, soil pH of the 0-10 cm layer showed the strongest correlation with the upper SOC stocks. With the exception of the FF under MOF, C storage increased significantly with increasing acidity. These results are consistent with other studies in tropical rainforests [Spain, 1990], and can be explained by several mechanisms. First, soil acidity allows OM stabilization through complexation of OM on mineral surfaces via ligand exchange [von Lützow et al., 2006]. Sec-

ond, soil acidity may inhibit soil microbial activities and therefore slow down the decomposition of OM [Motavalli et al., 1995]. Third, a decrease in soil pH might further reduce P availability by promoting its adsorption on positive hydroxyde charges [Brady and Weil, 2008].

Finally, because OM accumulation itself tends to reduce soil pH [Mueller et al., 2012] and to induce higher CN ratios, it would further reinforce the effects of the soil parameters.

2.4.4 General discussion: *G. dewevrei* impact

Analyses at both forest and subplot (within forest) levels highlighted the major role of the dominant tree species *G. dewevrei* on the carbon cycle. Because similar OM inputs were observed under both forest types, we conclude that the greater C accumulation in FF and MS under *G. dewevrei* results from a limitation of the decomposition rate. This was mainly attributed to a set of unfavourable litter traits, which could be re-enforced by a nutrient uptake strategy involving EM. This same set of traits was previously shown to be tightly linked with the monodominance of that species, at the expense of other tree species [Peh et al., 2011a].

On the other hand, comparing the below vs. aboveground C storage in MOF vs. MIF, it appears that the *G. dewevrei* induced limited nutrient availability under MOF, while promoting SOC storage, did not limit the AGC storage nor the net primary productivity (as inferred from similar C litterfall inputs) compared to MIF. This is probably the result of a very tight and efficient nutrient cycle, associated with a well-developed mycorrhizae network: the limited nutrient (P) returns through litterfall that would otherwise be expected to reduce productivity, are very efficiently captured by an extensive network of roots associated with mycorrhizal fungi, at the expense of the decomposer community. In the same time, the build-up of this FF layer contributes to the creation of an environment preventing the recruitment of other tree species [Peh et al., 2011a]. It thus appears that *G. dewevrei* presents a unique combination of traits

that produce very high species specific C storage in this ecological context, in agreement with the mass ratio hypothesis.

2.5 Conclusion

Despite similar ecological conditions, contrasting patterns of C accumulation were found between adjacent *Gilbertiodendron dewevrei* monodominant forests and *Scorodophloeus zenkeri* mixed forests in the Yoko reserve. The main difference was related to the much larger SOC stock under MOF that was not restricted to the FF and upper MS layers, but rather extended down to 1 m depth in the MS.

Because comparable C litterfall inputs and root mortality were recorded in both forest types, we conclude that the greater SOC accumulation under *G. dewevrei* at the forest level results from a limitation of the decomposition rate, in agreement with the traits of the associated leaf litter. More research would however be needed to assess of role of the roots and associated mycorrhizae, in terms of both litter quality and competition induced P limitation.

By contrast, our correlative approach suggests a limited involvement of litter and local stand attributes as possible drivers of upper SOC stocks within a forest type. This probably means that the range of leaf litter quality is too small at those local scales compared to other factors of C accumulation, such as woody debris or tree uprooting. Although soil parameters, including CN ratio and pH, were found to be correlated with SOC stocks, care should be taken when considering cause effects relationships as those two parameters are also expected to be influenced by OM accumulation.

Finally, as MIF and MOF co-exist on a large range of soils [Hart et al., 1989], it remains to determine whether the differences observed on those highly weathered sandy soils would be similar in other ecological contexts or whether difference in SOC accumulation would rather interact with site conditions.

Chapter 3

Tree species diversity in tropical wet forests produce highly diverse litter quality generating contrasted decomposition rates and mixture effects

Abstract

In nutrient-poor ecosystems as many tropical forests, litter decomposition is essential to nutrient availability, while influencing forest regeneration, plant productivity and carbon sequestration. The range of decay rates associated with a potentially very high number of tree species and their combinations is however still largely unknown. We collected freshly senesced leaf litter from 8 abundant species covering a large range of leaf traits in two emblematic oldgrowth forest types of the Central Congo basin: the *Scorodophloeus zenkeri* Harms mixed forests and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests. Initial leaf litter composition was characterized for 16 functional traits and litterbags with either monospecific litter (n=8) or all possible two-species combinations (n=28) were incubated for up to 6 months. The large variation in initial decomposition rate among species was better predicted by the position of the species along the leaf economics spectrum than by any single leaf litter traits. In agreement with the home field advantage theory, the initial decomposition rates (≤ 2 months) of the dominant species were accelerated under their own forest type, yet to a limited extent ($\leq 5\%$). The non-additive effects were greatly influenced by the decay stage and the presence of fast decomposing tree species in the mixture, while the chemical dissimilarity between the component species had only limited impacts. Altogether, these results pinpoints the need for an increased documentation of tree species leaf traits in tropical forests, especially in the Congo basin.

3.1 Introduction

The forest floor (FF) in forest ecosystems consists of a partially decomposed organic matter accumulated above the mineral soil. Boundary layer between the atmosphere and the mineral soil, FF plays a crucial role in forest functioning such as water and nutrient cycle [Rawls et al., 2003; Berg and McClaugherty, 2014]. In addition to serve as habitat for soil fauna, the litter layer can be more favourable to root development and nutrient uptake compared to the underlying mineral soil, especially in nutrient-poor ecosystems such as tropical forests. Indeed, tropical soils are highly weathered and provide limited amounts of nutrients required for trees nutrition. Therefore, as a source of energy for micro-organisms and a source of nutrients for plants, the dead organic matter in FF is the most favourable support for biological activity [Ghazoul and Sheil, 2010].

The accumulation of organic matter on forest ground is the net result of a sequence of several subprocesses. The input through litterfall, related to forest productivity, followed by the decomposition processes, leaving a certain fraction as stabilized residue. In forest ecosystems, litter decomposition and nutrients dynamics are determined by multiple key drivers including climate, litter quality, site-specific factors (such as soil properties) and the decomposer community [Coûteaux et al., 1995; Aerts, 1997; Hättenschwiler et al., 2005; Cornwell et al., 2008]. For a given site, litter chemical and physical quality explains most of the reported variation in litter decomposition rate.

Litter decay rate is controlled by a wide variety of litter functional traits including N and P concentration and lignin fraction or lignin to nutrient ratios [Wieder et al., 2009]. Indeed, C, N and P are key elements for growth and activity of the decomposers [Manzoni et al., 2010]. In tropical forests, where P is the most limiting nutrient for plant growth, P concentration and the lignin:P ratio could have a stronger impact on litter decomposition in contrast to temperate forests where N concentration is the main driver [Cleveland et al., 2002]. However, Aerts [1997] high-

lighted that nutrient control over litter break down changed over time; decay rate during early stage was strongly driven by all P-related litter traits, whereas long-term litter decay was most controlled by secondary compounds (e.g. lignin), that are relatively resistant to degradation.

The pattern of correlations among plant functional traits is strikingly consistent across and within species at both small and large scales and is described as the leaf economics spectrum (LES). The LES is frequently used to describe life-history strategy [Poorter and Bongers, 2006; Donovan et al., 2011]. On one-side, the LES is dominated by fast-growing species that produce short-lived, structurally inexpensive leaves consisting of high leaf-level photosynthetic rates and N concentrations, and low leaf mass per area. At the opposite side, we find slow-growing and long-lived species that exhibit "resource conserving" traits such as high leaf mass per area and low nutrient concentration. Bakker et al. [2011] have shown that plant species position across the LES was strongly related to their decay rate under different land use types in the tropics.

Evidence is growing that litter decay rate is improved in the habitat from which the litter was derived compared to other habitat, which has been termed the "home field advantage" (HFA) [Austin et al., 2014; Veen et al., 2015; Chomel et al., 2015]. This HFA is mainly explained by the close specialisation of decomposers for the litter to a certain plant community [Negrete-Yankelevich et al., 2008]. HFA effect has been shown to increase with greater dissimilarity in litter quality and in plant communities across sites [Ayres et al., 2009; Freschet et al., 2012a].

Most studies focusing on litter decomposition dealt with the breakdown of single-species litter, but forest ecosystems often contain multiple tree species leading to a litter layer with leaves from a number of species, especially in tropical rainforest well known to exhibit the most species-rich plant communities. In such ecosystems, strong interspecific variation in foliage quality and stoichiometry have been reported at local and regional scales [Townsend et al., 2007; Hättenschwiler et al., 2008] resulting in a chemically and physically highly diverse litter input. When litter from different species coexist, decomposition rates can differ from expecta-

tions based on observations made on corresponding single species litters [Gartner and Cardon, 2004; Coq et al., 2011; Setiawan et al., 2016]. Mixing litter can have no effect (additivity) or either enhance or decelerate decomposition (non-additivity). When non-additive mixing effects occurs, differences of 20-30% between observed and predicted mass loss are not uncommon [Hättenschwiler et al., 2005].

Although numerous litter mixtures show non-additive effects, the factors and processes that control these mixing effects are still debated [Gessner et al., 2010; Lecerf et al., 2011; Frainer et al., 2015]. Number of species in litter mixtures often appeared to be a poor predictor for deviations from expectation [Wardle et al., 1997; Tardif and Shipley, 2013]. Conversely, interaction effect in mixing litters may be caused by the chemical heterogeneity of the litter mixture or by variation in the decomposition microenvironment [Schimel and Hättenschwiler, 2007; Jonsson and Wardle, 2008; Makkonen et al., 2013]. Some studies showed that stronger non-additive effects were reported when the component species exhibit contrasted litter traits [Lecerf et al., 2011; Barantal et al., 2014; Finerty et al., 2016]. However, mixture effects in litter decomposition were generally studied with a litterbag approach considering all litter components as a whole without measuring the mass loss of each litter separately. Due to compensation effects, this may mask species-specific responses to mixing litter [Prescott et al., 2000; Wardle et al., 2003]. Potential mechanisms to explain the non-additive effects involve nutrient translocation between litter types, resource complementary, change in microbial and detritivore populations due to new development conditions [Hättenschwiler et al., 2005; Gessner et al., 2010]. All these mechanisms are intimately linked to the litter quality of the species involved in the mixture suggesting a strong species identity effect (Hoorens et al. 2010). Active nutrient transport occurs when fungi growing in nutrient-poor litter can take up limiting nutrient by extending their hyphae to nutrient richer component species [Schimel and Hättenschwiler, 2007]. Nutrients can also be transported in a passive way by diffusion or water flow. Not only nutrients but also inhibitory compounds can be transferred from a litter to another leading to negative effects on decomposition.

Whereas tropical rainforests exhibit high tree species richness with up to 300 tree species per ha [Sullivan et al., 2017], old-growth forests where nearly one single tree species dominates in the upper canopy layer, the so-called "monodominant forests" [Connell and Lowman, 1989], are commonly found alongside such diverse forest. *Gilbertiodendron dewevrei* is a tree species which dominates large patches in Central Africa. These monodominant forests (MOF) are often adjacent to *Scorodophloeus zenkeri* mixed forests (MIF). These two forest types cover extensive areas in the zone, where they frequently co-occur on similar ecological conditions on a wide variety of soils [Hart et al., 1989; Djuikouo et al., 2010; Kearsley et al., 2017]. The dominance of *G. dewevrei* was previously shown to be tightly linked with a set of unfavourable litter traits, limiting the development/growth of other tree species [Peh et al., 2011a]. In addition, Cassart et al. [2016] demonstrated that strong soil organic carbon (forest floor and mineral soil) accumulation under MOF was related to these traits.

In this study, we assessed litter traits and decomposition rate of the eight most abundant species under MIF and MOF in pure litters and in two-species mixtures involving all possible combinations in a forest area of the Central Congo basin. More precisely, we aim at identifying the drivers which control decay rates in single-species and mixed litterbags.

We hypothesized that:

1. To evaluate litter quality effects on decomposition, tree species position along the LES is a better predictor of decay rate than individual traits
2. In agreement with the HFA hypothesis, *S. zenkeri* and *G. dewevrei* litter decomposition are favoured under MIF and MOF, respectively
3. Synergistic litter mixture effects on decomposition increase with stoichiometric dissimilarity of leaf litter mixtures.

3.2 Materials and methods

3.2.1 Study site

This study was conducted in the Yoko Forest Reserve in the Tshopo province of the Democratic Republic of Congo (DRC). The Reserve is located on a sandy plateau at about 28 km south of Kisangani (N 00 19'12"; E 25 17'43") and 450 m of elevation, and covers an area of 6975 ha.

According to the revised Köppen-Geiger classification, the regional climate is described as Af-type tropical rainforest climate [Peel et al., 2007]. Based on the meteorological data collected from the Yangambi station (located 100 km to the west of Kisangani) between 1961 and 2009, mean annual rainfall is 1780 (± 230) mm with two distinct rainy seasons (March-June and August-December), and a cumulated dry season length of *ca* 3 months (January-February and July) with monthly precipitation lower than 60 mm. The mean annual air temperature is 24.8°C with limited seasonal variability. The dominant soil type is classified as Xanthic Ferralsol [Van Ranst et al., 2010; WRB, 2014] mostly composed of quartz sand, with low content of kaolinite clay and hydrated iron oxides.

The vegetation of the reserve is dominated by pristine moist semi-deciduous rainforest mixed with variable patches of moist evergreen rainforests. Few transition forests and slash-and-burn agriculture areas are found on the west side of the reserve, along the road.

A preliminary survey allowed us to select areas of the Reserve dominated either by semi-deciduous *Scorodophloeus zenkeri* Harms mixed forests (MIF) or by evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF), in otherwise similar topographic and edaphic conditions. While the stand basal area, stand density and soil characteristics were comparable between both forest types (cf. Table 2.1 in chapter 2), species composition and diversity strongly differed. Both MIF and MOF are on nutrient poor ($\text{CEC} \leq 5.3 \text{ cmol}_c \text{ kg}^{-1}$) and strongly

acidic soil ($\text{pH} \leq 4.2$) with high total sand (coarse + fine) content ($>86\%$) in topsoil.

3.2.2 Litter decomposition experiment

Eight tree species were involved in the experiment: *Anonidium mannii* (Oliv.) Engl. & Diels, *Cynometra hankei* Harms, *Gilbertiodendron dewevrei* (De Wild.) J.Léonard, *Guarea thompsonii* Sprague & Hutch., *Julbernardia seretii* (De Wild.) Troupin, *Polyalthia suaveolens* Engl. & Diels, *Prioria oxyphylla* (Harms) Breteler, *Scorodophloeus zenkeri* Harms; with the exception of *G. dewevrei*, all those species are found in both forest types. These tree species accounted for 48.7 and 84.6% of total basal area in MIF and MOF respectively. They were chosen to maximise the range of leaf functional traits, especially CN ratio and were supposed to decompose at different rates. Leaf litter of these tree species was collected in litter traps randomly placed in MIF and MOF during peak litter fall (February 2014) and were pooled and homogenized per tree species; if necessary, newly senescent leaves were collected from the forest floor. All leaf litter material was directly air-dried in the field and further oven-dried at 40°C in the lab and stored until further use. Sub-samples of litter from each tree species were oven-dried at 65°C during 48h to determine their water content and convert fresh litter mass into dry litter mass.

Litterbags (15x15 cm) were made from plastic insect screen with ± 2 mm mesh size. This mesh size avoids litter fragments losses while still allowing access to mesofauna [Swift et al., 1979]. Each litterbag received a total mass of 13 g dry litter, equivalent to 580 g m^{-2} , which is consistent with annual aboveground litterfall input in MIF and MOF (see chapter 2). To preserve the leaf structural properties, leaves were not ground or cut, except *G. dewevrei*, which was cut into 15 cm lengths to fit into the litterbags.

In order to investigate individual leaf litter decay rate, we incubated pure litter of each studied tree species ($n=8$) under MIF. Litterbags were in-

cubated in 5 blocks approximatively 100 meters apart, each divided into 2 replicates (1 m x 1m) that were several meters apart. For each tree species, 40 bags were prepared: 5 blocks x 2 replicates x 4 retrieval dates. A possible HFA effect was assessed by incubating pure litter of the two dominant species (*G. dewevrei* and *S. zenkeri* for MOF and MIF, respectively) under MOF with the same design (5 blocks and 2 replicates per block). Finally, to test for possible interacting effects among litters, mixed litter bags corresponding to all two-way combinations of the tree species (n=28; Table 3.3) were incubated in one replicate per block under MIF; for every litter mixture, 10 bags were prepared: 5 blocks x 2 retrieval dates.

The litterbags were placed on the forest floor in September 2014 (at the end of the dry season, when forest floor litter mass was highest) and were attached to the forest floor by metal pins to prevent movement. Pure litterbags were retrieved after 1, 2, 3 and 6 months and mixed litterbags after 1 and 6 months. Following collection, litterbags were air-dried and litter was removed from each litterbag. Adhered debris were removed and adhering sand particles rinsed with water. The contents of mixed litterbags were separated by species to assess individual species mass loss in mixture. Litter were oven-dried at 65°C during 48h and weighed.

3.2.3 Leaf litter trait measurement

Composite subsamples of newly senescent leaf litter from each tree species were air-dried, grinded and stored (at room temperature away from light and humidity) for chemical analyses. C and N concentrations of each sample were measured with a Flash EA CN 1112 series elemental analyser. Ca, K, Mg, Mn, P, S and Si concentrations were determined by inductively coupled plasma spectrometry following total acid digestion (a mixed solution of nitric and hydrofluoric acids) in a Milestone UltraWAVE microwave digestion system. Lignin and cellulose contents were determined based on the method proposed by Van Soest and Wine [1967], using a Gerhardt FibreBag apparatus.

3.2.4 Calculations and statistical analysis

Relative remaining litter mass (RM, %) at harvest time 't' was calculated as

$$RM = \frac{m_t}{m_0} \times 100 \quad (3.1)$$

where m_t indicates the dry mass of each litter component at harvest time 't' and m_0 the initial dry mass of each litter component in the litterbags. For the single-species litterbags, RM was modelled by species as a function of time using the following time-dependent model in which the decay rate is time-dependent [Feng and Li, 2001; Manzoni et al., 2012] :

$$RM_t = e^{-\left(\frac{t}{b}\right)^a} \times 100 + \varepsilon \quad (3.2)$$

with a and b parameters describing the shape of the curve. Temporal autocorrelation was accounted for in our model. Contrary to the single exponential model developed by Olson [1963] using a constant decay rate over the decomposition period, the form of Eq. 3.2 allows the decay rate to change (increase and decrease) with time according to the decomposition processes. Based on Eq. 3.2, the instantaneous and apparent decay rate (k_{app} , expressed as month⁻¹) can be computed as:

$$k_{app} = \frac{a}{b} \left(\frac{t}{b}\right)^{a-1} \quad (3.3)$$

Because of strong correlation between traits, the relationships among variables of litter quality were explored using a principal component analysis (PCA) with 11 foliar litter traits (C, Ca, Cellulose, K, lignin, Mg, Mn, N, P, S, Si litter concentrations), using species ($n = 8$) as data points. Lignin:N (L:N), C:N, C:P, C:S and N:P ratios were included as supplementary variables and did not affect the ordination. Initial nutrient concentrations of mixtures were calculated as the average concentration of its component species, and the positions of the different litter mixtures were also included as supplementary individuals.

We used linear regressions to determine how well initial litter chemistry can predict k_{app} in monospecific litterbags and RM in mixed litterbags. Initial litter chemistry was characterized based on the scores of the first two PCA axes and on the individual tree species traits. Given the high proportion of the variance explained by the first PCA axis, the latter was used as an integrated and quantitative measure of the "leaf economics spectrum scores" [Wright et al., 2004].

We calculated expected RM of litter mixture each litter component based on the single-species decomposition experiment at same harvest time. As both species are in equal proportions in mixture, the expected RM of the whole mixture is the average of the expected RM of the two components. Deviation from the expected RM (DERM) of the mixture as a whole ($DERM_m$), or of each component of the mixture (the target species - $DERM_t$ *vs.* the neighbour species - $DERM_n$) were calculated as:

$$DERM = \frac{RM_{Expected} - RM_{Observed}}{RM_{Expected}} \times 100 \quad (3.4)$$

Negative DERM values suggest antagonistic responses (decreasing litter breakdown), whereas positive values refer to synergistic responses (acceleration of litter decomposition). The effect of mixing on the decomposition of one target tree species was quantified by the DERM value of that species averaged over all mixtures containing that species ($DERM_t$). Similarly, the impact of one species on the decomposition of its neighbours was assessed by the DERM value of the neighbours over all mixtures containing that species ($DERM_n$).

The effect of chemical dissimilarity (CD_m), decay stage (DS_m) and maximum relative decomposition index of the mixture ($MRDI_m$) on $DERM_m$ was quantified using linear mixed effects model with the block as random effect in which we allowed coefficient to vary in function of time. Coefficients after 1 and 6 months were then compared using a t-test.

CD_m between component species of the mixture was measured as the distance between species in the four factor PCA space. These four factors explained more than 92% of the variability in the 11 leaf litter traits

among the eight tree species involved. The DS_m was calculated as 100 minus its relative remaining litter mass. Maximum relative decomposition index of the mixture ($MRDI_m$) was calculated as:

$$MRDI_m = \frac{100 - RM_{min}}{100 - RM_{mean}} \quad (3.5)$$

where RM_{min} is the minimum RM between the two components of the mixture and RM_{mean} the average RM of the two species composing the mixture but considered across every mixture for the corresponding period of measurements. High $MRDI_m$ indicate the presence of easily decomposable litter in the mixture.

All statistical analyses were performed in R version 3.2.0.

3.3 Results

3.3.1 Litter quality

Across the studied species, a wide variability in initial leaf litter traits was observed (Table 3.1). For example, Mn concentrations varied 120-fold among species, from 0.03 (*G. dewevrei*) to 3.57 mg g⁻¹ (*P. oxyphylla*) and K concentrations varied 9-fold, from 2.58 (*P. oxyphylla*) to 24.09 mg g⁻¹ (*G. thompsonii*). Differences from 2 to 8-fold were observed for the other leaf litter traits.

The first two axes of the PCA explained 67.1% of the variability in the 11 leaf litter traits among the eight tree species involved in the decomposition experiment (Figure 3.1a). The first axis accounted for the large majority of this explained variability (48.6%) and was positively related to litter Ca, K, Mg, N, P and S concentrations and negatively related to C, lignin and Si concentrations. The second axis explained an additional 18.5% of the variability in traits and was positively related to Cellulose and Mn concentrations.

C. hankei, *G. dewevrei*, *J. seretii* and *P. oxyphylla* were found at the left side of the first PCA axis and therefore exhibited lower nutrient concen-

Table 3.1 – Average leaf litter composition for the pool of 8 tree species used in the decomposition experiments

(a)

Species	Nutrient (mg g ⁻¹)							
	N	Ca	K	P	Mn	Mg	S	Si
<i>A. mannii</i>	27.45	7.73	4.97	1.42	1.85	3.42	5.79	5.98
<i>C. hankei</i>	25.85	8.25	6.58	1.20	1.23	1.25	1.72	9.50
<i>G. dewevrei</i>	14.5	5.43	4.01	0.56	0.03	2.18	1.27	24.44
<i>G. thompsonii</i>	29.19	13.59	24.09	2.45	0.11	3.19	4.89	7.22
<i>J. seretii</i>	15.00	8.20	4.11	0.61	2.70	1.74	2.69	20.20
<i>P. suaveolens</i>	31.23	10.70	7.86	1.33	3.11	3.09	5.43	7.32
<i>P. oxyphylla</i>	16.31	11.51	2.58	0.59	3.57	2.24	1.99	11.21
<i>S. zenkeri</i>	30.68	14.01	7.65	1.51	3.50	3.21	9.72	17.45

(b)

Species	C fraction (mg g ⁻¹)		Ratios			
	Lignin	Cellulose	C:N	C:S	N:P	L:N
<i>A. mannii</i>	287.24	435.87	17.99	85.30	19.33	10.46
<i>C. hankei</i>	507.88	344.91	20.14	302.01	21.52	19.65
<i>G. dewevrei</i>	391.72	338.00	33.82	385.20	25.86	27.00
<i>G. thompsonii</i>	261.78	302.38	16.69	99.66	11.90	8.97
<i>J. seretii</i>	399.00	352.07	33.55	186.78	24.60	26.60
<i>P. suaveolens</i>	348.43	335.36	16.27	93.67	23.56	11.15
<i>P. oxyphylla</i>	402.07	385.07	30.59	251.10	27.42	24.65
<i>S. zenkeri</i>	302.67	328.44	15.45	48.78	20.25	9.87

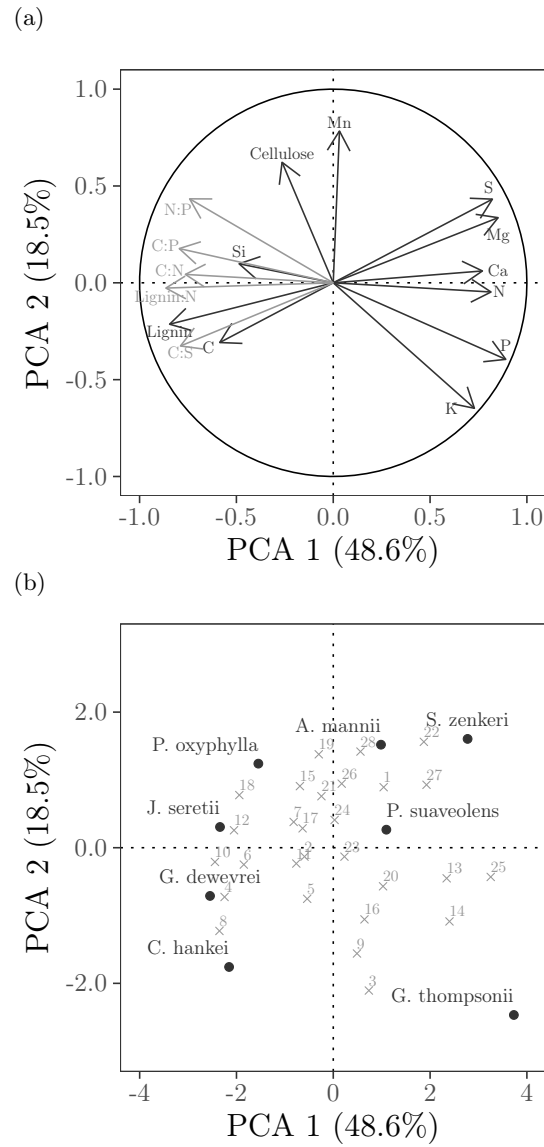


Figure 3.1 – Principal component analysis of 16 leaf litter traits of 8 tropical tree species (black points). Traits included as active variables in the analysis (black arrows): C, Ca, K, Mg, Mn, N, P, S, Si, Cellulose and lignin litter concentrations. Traits included as illustrative variables (grey arrows): C:N, C:S, C:P, N:P, and lignin:N litter ratios. The positions of the litter mixture (from 1 to 28, see Table 3.3) are included as supplementary individuals

trations and higher lignin concentration (Figure 3.1b). *G. dewevrei* had the lowest N, Ca, K, P, Mn and Mg but the highest Si litter concentrations. *A. mannii*, *G. thompsonii*, *P. suaveolens* and *S. zenkeri* were found at the right side of the first PCA axis and showed higher Ca, K, Mg, N, P and S concentrations. *S. zenkeri* exhibited the highest N, Ca, Mg and S litter concentrations. *G. thompsonii* was associated with the highest K and P concentrations, and the lowest lignin fraction as well as N:P and lignin:N ratios.

3.3.2 Chemical controls on litter decomposition rate in single-species litterbags

After 6 months of incubation, the remaining mass varied from 27.18 (*G. thompsonii* and *S. zenkeri*) to 56.44% (*G. dewevrei*; Figure 3.2a). The highest mass loss occurred during the first month of decomposition where mass loss varied between 5.88 and 38.24%, for *G. dewevrei* and *S. zenkeri*, respectively. Litter decomposition showed strong changes in early stage whereas mass loss between the 3rd and the 6th months ranged between 16.87 and 23.13% of the initial litter mass (for species-specific RM time-dependent model, see Appendix 12).

The highest decay rates (k_{app}) during the first month of decomposition were shown by *S. zenkeri* and *G. thompsonii* (0.24 and 0.25 month⁻¹, respectively) but this rate decreased quickly and reached values of 0.11 and 0.12 month⁻¹ after 6 months for *S. zenkeri* and *G. thompsonii*, respectively (Figure 3.2b). Moderate decay rates were shown by *P. suaveolens*, *A. mannii*, *J. seretii*, *P. oxyphylla* and *C. hankei* (0.17, 0.14, 0.13, 0.13 and 0.11 month⁻¹, respectively) and remained relatively stable over the duration of the experiment. The decay rate of *G. dewevrei* was initially the lowest and then stabilized around that of the other tree species after 6 months. After 6 months of decomposition, decay rates were stabilizing around 0.12 month⁻¹, except for *P. suaveolens* lying at 0.16 month⁻¹. Decay rates differed significantly among species at 1, 2 and 3 months (ANOVA for t=1: F=11.54; P<10⁻⁵) but difference decreased with time;

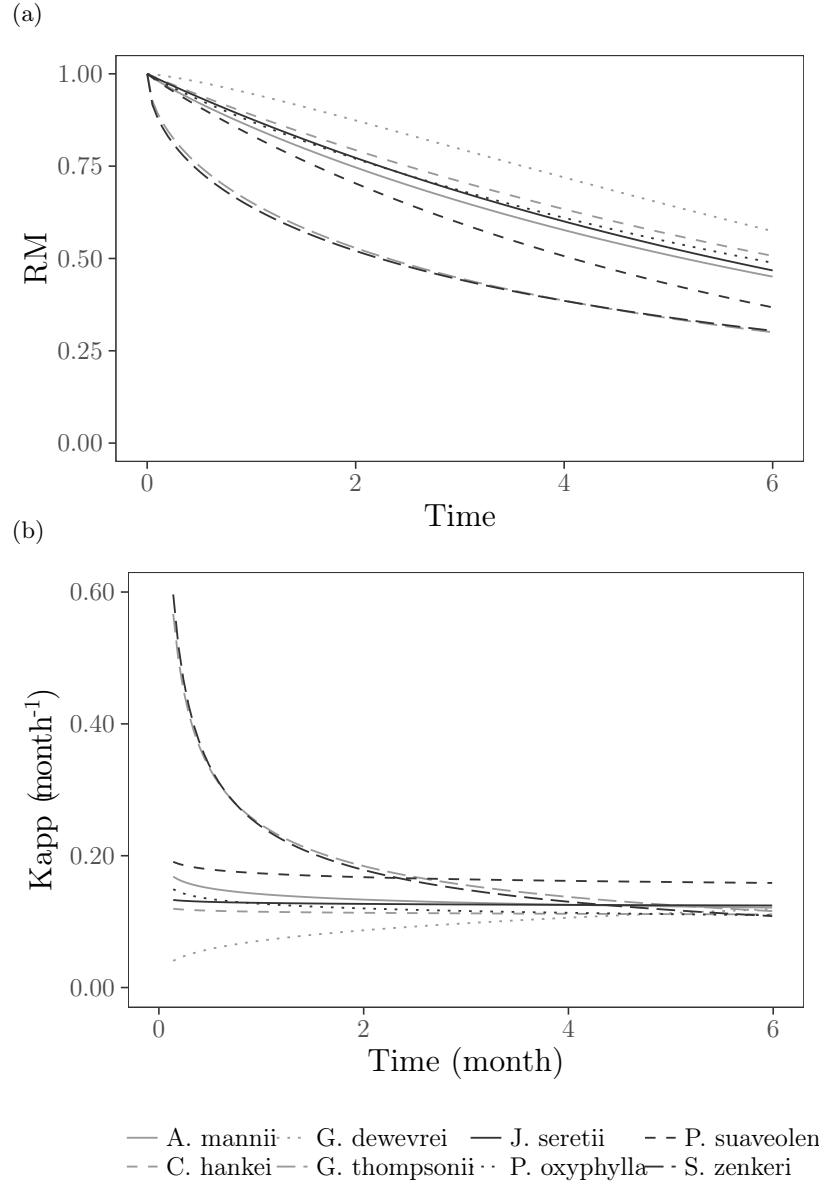


Figure 3.2 – (a) Remaining Mass (RM) and (b) apparent decay rates (k_{app}) as a function of time. Apparent decay rates were calculated using $k_{app} = (a/b) \times (t/b)^{(a-1)}$ where parameters (a,b) were adjusted based on the relationship between remaining mass (RM) and time (t): $RM = \exp(-(t/b)^a)$

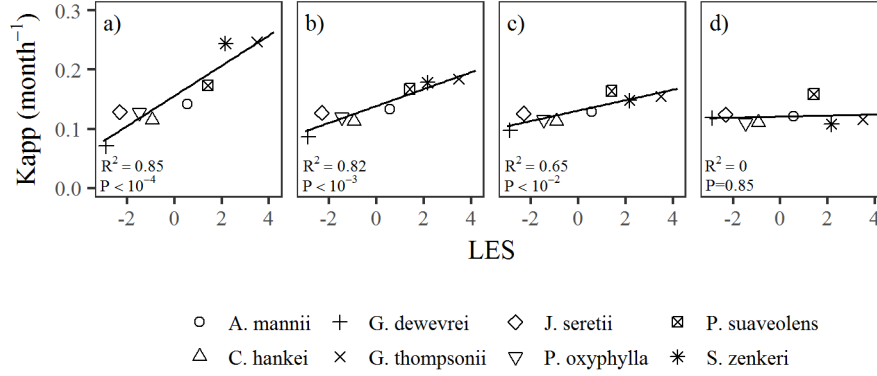


Figure 3.3 – Litter apparent decay rates (k_{app}) under MIF at 1 (a), 2 (b), 3 (c) and 6 (d) months for 8 tropical tree species as a function of species position on the leaf litter economics spectrum (LES) in the Yoko Reserve

decay rate did not vary significantly with species after 6 months (ANOVA for $t=6$: $F=0.828$; $P=0.56$).

Up to the 3rd month, the initial litter quality, characterized by the species position along the LES, was a good predictor for the decay rate (Figure 3.3) but the impact of initial litter quality on decomposition rate decreased with time ($R^2=0.85$, 0.82 and 0.65 for $t=1$, 2 and 3 , respectively). After 6 months, the relationship between the species position on the LES and decay rate became non-significant ($R^2=0.00$; $P=0.85$), which is consistent with the previously reported non-significant effect of tree species on k_{app} after 6 months.

Interspecific variation in decay rate was also significantly associated with individual leaf litter traits (Figure 3.4). Initial leaf litter Ca concentration was found to have the greatest influence among individual traits ($R^2=0.79$; $P=0.002$; Figure 3.4a), followed by P concentration ($R^2=0.64$; $P=0.01$; Figure 3.4b), S concentration ($R^2=0.61$; $P=0.01$; Figure 3.4c) and lignin:N ratio ($R^2=0.51$; $P=0.03$; Figure 3.4d). Decomposition rate was also related to other individual leaf litter traits and a summary of the relationships between k_{app} and N, K, lignin, Mg concentration and C:S

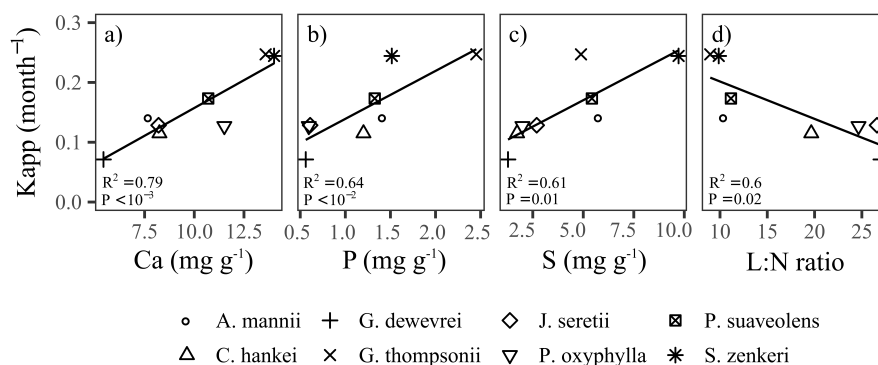


Figure 3.4 – Litter apparent decay rates (k_{app}) after 1 month of incubation under MIF for 8 tropical tree species as a function of litter Ca (a), P (b) and S (c) concentrations and litter lignin:N ratio (d) in the Yoko Reserve. The relationships between k_{app} and the other leaf litter characteristics are given in Appendix 13

and N:P ratios is available in Appendices (see Appendix 13). No significant relationships were found between k_{app} and leaf litter concentrations in Cellulose, Mn and Si.

3.3.3 Impact of environment on litter decomposition

Based on the data in Table 3.2, mass loss of *G. dewevrei* was slightly but significantly higher under MOF compared to MIF in the first two months of decomposition (mean difference around 5 and 4% after 1 and 2 months, respectively) and became similar in MIF and MOF after 3 months of incubation. On the contrary, mass loss of *S. zenkeri* was significantly higher under MIF compared to MOF (mean difference around 5 and 9% after 1 and 2 months, respectively) but, as observed for *G. dewevrei*, differences between forests became non-significant after 3 months.

Table 3.2 – Remaining litter mass of *G. dewevrei* and *S. zenkeri* after 1, 2, 3 and 6 months of incubation under MIF and MOF (mean $\pm$ standard deviation). p-values refer to the forest type effect

(a)

Time (months)	<i>G. dewevrei</i>		p-values
	MIF	MOF	
1	94.12 $\pm$ 4.74	89.19 $\pm$ 5.15	0.03
2	90.06 $\pm$ 2.33	85.53 $\pm$ 4.68	<0.01
3	79.58 $\pm$ 5.12	78.22 $\pm$ 3.73	0.49
6	56.45 $\pm$ 4.36	58.82 $\pm$ 5.07	0.25

(b)

Time (months)	<i>S. zenkeri</i>		p-values
	MIF	MOF	
1	61.76 $\pm$ 4.74	67.10 $\pm$ 4.80	0.01
2	51.36 $\pm$ 2.83	60.53 $\pm$ 7.99	<0.01
3	49.31 $\pm$ 13.1	49.81 $\pm$ 4.90	0.91
6	27.72 $\pm$ 3.86	31.00 $\pm$ 4.06	0.06

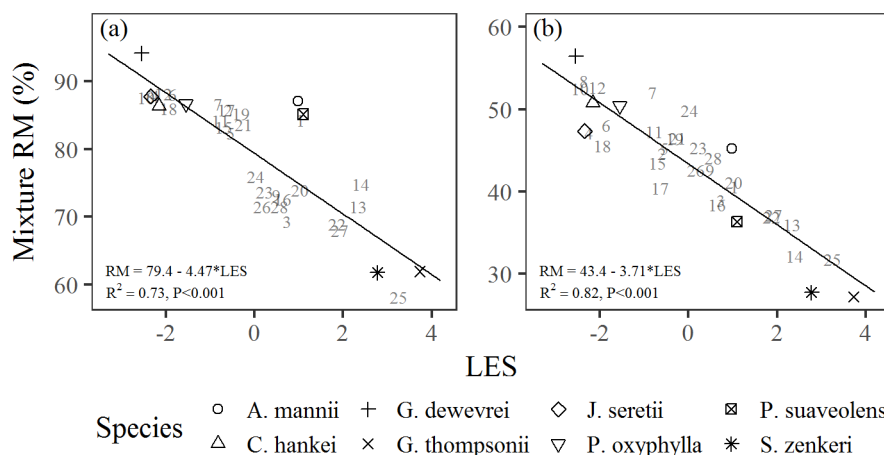


Figure 3.5 – Remaining litter mass in pure (black shapes) and mixed (grey numbers from 1 to 28, see Table 3.3) litterbags under MIF after (a) 1 and (b) 6 months of incubation as a function of mixture position on the litter leaf economics spectrum (LES) in the Yoko Reserve (see Figure 3.1)

3.3.4 Litter mixing effects on remaining mass

RM in mixed litterbags was strongly negatively related to the position of the mixture on the LES after 1 ($R^2=0.73$, $P<10^{-3}$) and 6 ($R^2=0.82$, $P<10^{-3}$) months of incubation (Figure 3.5).

DERM_m changed with decomposition time; DERM_m first showed significant synergistic mixing effect after 1 month (mean DERM_m across all 28 mixture types: +3.21%, $P<10^{-5}$) while after 6 months of incubation mixing effect became antagonistic but not significant (mean DERM_m across all 28 mixture types: -2.65%, $P=0.06$). When fitting DERM_m with CD_m, DS_m and MRDI_m using linear mixed model with the block as random effect, we could explain about 71% of the variation in DERM_m (Table 3.4). DS_m and CD_m were significantly positively related to DERM_m while DERM_m decreased significantly with increasing MRDI_m. The effects of CD_m, DS_m and MRDI_m on DERM_m significantly differed after 1 or 6 months of incubation.

Table 3.3 – Deviation from the expected RM ($DERM_m$, %) and chemical dissimilarity (CD_m) of the mixture under MIF. Negative $DERM_m$ values indicate antagonistic responses (decreasing litter breakdown), whereas positive values refer to synergistic responses (acceleration of litter decomposition). +, *, **, *** denote $DERM_m$ respectively significantly different from zero at $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$

ID	Mixture	$DERM_m$ (%)		CD_m
		t=1	t=6	
1	A. mannii + P. suaveolens	2.13	0.62	1.64
2	C. hankei + A. mannii	1.15	7.00 **	3.55
3	C. hankei + G. thompsonii	6.77 *	0.77	5.47
4	C. hankei + J. seretii	-0.9	3.9	2.97
5	C. hankei + P. suaveolens	3.99 +	-3.82	3.19
6	C. hankei + P. oxyphylla	-1.78	5.1	3.47
7	G. dewevrei + A. mannii	4.42 *	-2.17	5.38
8	G. dewevrei + C. hankei	2.86 *	0.35	4.80
9	G. dewevrei + G. thompsonii	6.84 *	-0.76	6.97
10	G. dewevrei + J. seretii	3.75 **	-1.05	3.00
11	G. dewevrei + P. suaveolens	6.19 *	-1.45	6.00
12	G. dewevrei + P. oxyphylla	2.52 +	1.49	3.97
13	G. thompsonii + A. mannii	4.21 **	0.87	4.23
14	G. thompsonii + P. suaveolens	-1.62	-0.99	4.25
15	J. seretii + A. mannii	4.82 **	6.11 *	3.84
16	J. seretii + G. thompsonii	3.17 ***	-2.54	6.31
17	J. seretii + P. suaveolens	0.7	3.52	3.78
18	J. seretii + P. oxyphylla	1.35	6.87 **	1.49
19	P. oxyphylla + A. mannii	1.94	3.01	4.28
20	P. oxyphylla + G. thompsonii	0.88	-5.13	6.11
21	P. oxyphylla + P. suaveolens	2.71 +	-6.98	3.72
22	S. zenkeri + A. mannii	7.48 **	-0.89	3.36
23	S. zenkeri + C. hankei	1.07	-14.42 **	6.14
24	S. zenkeri + G. dewevrei	3.20 *	-17.09 **	6.79
25	S. zenkeri + G. thompsonii	5.93 *	-15.62 ***	4.63
26	S. zenkeri + J. seretii	4.59 **	-13.05 *	5.28
27	S. zenkeri + P. suaveolens	7.61 **	-15.87 +	3.35
28	S. zenkeri + P. oxyphylla	4.00 **	-11.97 +	4.93

Table 3.4 – Parameter estimates and R^2 of the fixed part of the linear mixed model quantifying the effects of chemical dissimilarity (CD_m), decay stage (DS_m) and maximum relative decomposition index ($MRDI_m$) of the mixture on its deviation from expected RM ($DERM_m$) with the block as random effect. *, **, *** denote respectively significant difference from zero at $p < 0.10$, $p < 0.05$, $p < 0.01$ and $p < 0.001$. Different letters in a row indicate significant difference between measurement dates ($p < 0.05$). No incubation time effect was found for the intercept

Model terms	Time (months)		R^2
	1	6	
Intercept	$-6.55 \pm 1.39^{***}$		
CD_m	$0.99 \pm 0.33^{*,a}$	$2.15 \pm 0.35^{***,b}$	0.71
DS_m	$0.82 \pm 0.09^{***,a}$	$1.48 \pm 0.07^{***,b}$	
$MRDI_m$	$-8.84 \pm 1.37^{***,a}$	$-80.03 \pm 4.13^{***,b}$	

If we consider the whole mixture, the effect of the presence of target species on $DERM_m$ was relatively small and differed with time (Figure 3.6a). After 1 month, mass loss of the mixture was significantly enhanced by the presence of the target species for each mixture. After 6 months, mass loss of the mixture was significantly reduced only by the presence of *S. zenkeri*, *G. thompsonii*, *P. suaveolens* or *G. dewevrei* (Table 3.3, Figure 3.6a). Strongest $DERM_m$ was reported for mixtures including *S. zenkeri* and reached 4.75 ± 0.57 and $-12.92 \pm 1.76\%$ after 1 and 6 months, respectively.

Figure 3.6b shows the effects of the target species identity in the mixtures on the remaining mass of the neighbour. *S. zenkeri*, *C. hankei* and *G. dewevrei* first significantly enhanced litter decomposition of their neighbours but subsequently strongly reduced litter mass loss of their neighbours. *G. thompsonii* was the only species to significantly boost the decomposition of its neighbour after 1 and 6 months. The presence of *P. oxyphylla* and *P. suaveolens* in mixture did not affect significantly the decomposition of the other species. *A. mannii* and *J. seretii* affected only the litter mass loss of their neighbour after 6 and 1 months, respectively.

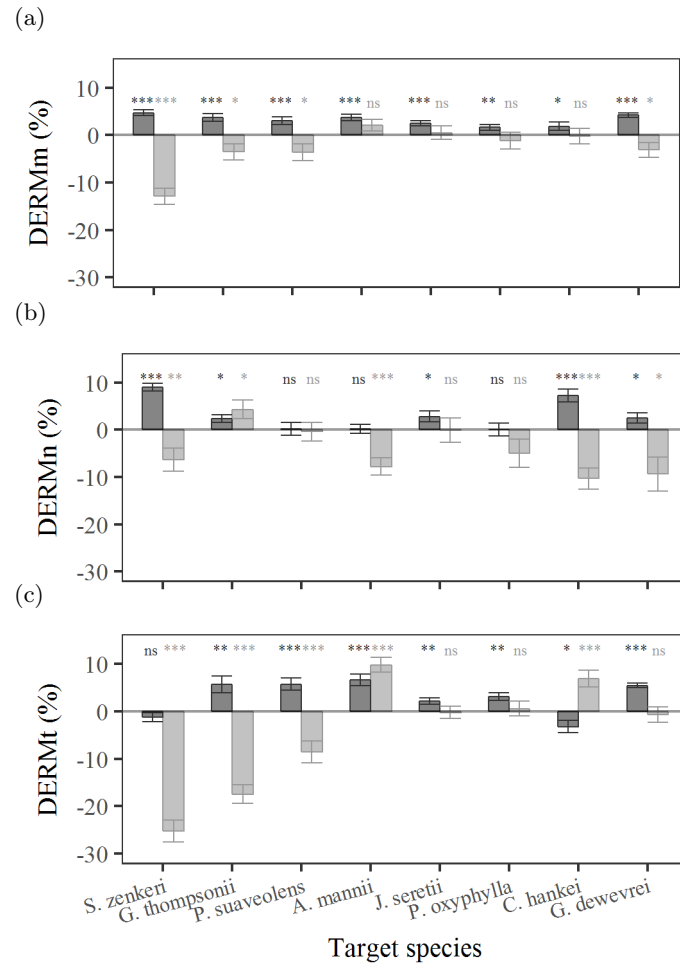


Figure 3.6 – Mean deviation from the expected relative remaining litter mass after 1 and 6 months (in black and gray, respectively) for a) the whole mixture (DERM_m) in presence of the target species, b) the neighbor species in the mixture (DERM_n) in presence of the target species and c) the target species in the mixture (DERM_t). Species are ordered according to their k_{app} after 1 month of incubation. Means and SE are shown. 'ns' indicates DERM is not significantly different from zero; *, **, *** denotes DERM significantly deviates from zero at $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively

The pattern of the decay rate of the target species in mixture strongly varied with species identity and time (Figure 3.6c). Litter mass loss of *A. mannii* was significantly enhanced by mixing after 1 and 6 months of incubation. *C. hankei* decomposition was first significantly reduced and next enhanced by mixing, inverse pattern was reported for *G. thompsonii* and *P. suaveolens*. Litter mass loss of *G. dewevrei*, *J. seretii* and *P. oxyphylla* was slightly but significantly increased after 1 month by mixing (DERM_t from 2.15 to 5.71 %). Strongest negative DERM_t were reported for *G. thompsonii* and *S. zenkeri* after 6 months of incubation (-17.45 and -25.23 %, respectively).

3.4 Discussion

3.4.1 Temporal dynamic and interspecific variation of litter decay

Under MIF, the average litter decay rates across species were 0.12 month⁻¹ after 6 months indicating that 57% of litter mass was lost in 6 months. As expected, this value is higher compared to decomposition rate reported in temperate forests but similar to mean value of 0.19 month⁻¹ (range 0.04-0.32) observed in tropical forests for the same reference period [Aerts, 1997; Hättenschwiler et al., 2011; Waring, 2012].

A greater mass loss was reported for *S. Zenkeri* and *G. thompsonii* with 72 and 73% of mass loss after 6 months of incubation, respectively. *G. dewevrei* exhibited the lowest decomposition rate during early decomposition stages. The limited mass loss of *G. dewevrei* under MIF observed in this study (20% after 3 months) is consistent with the range of mass losses reported in previous studies [Torti et al., 2001; Peh et al., 2012]. Several studies suggest that the slow litter decomposition of *G. dewevrei*, by inhibiting the establishment of small-seeded species and causing a low N availability, is a key part of its dominance strategy [Hart et al., 1989; Peh et al., 2011a;b]. In addition, Cassart et al. [2016] have shown that greater soil (forest floor and mineral soil) carbon accumulation under

MOF compared to adjacent mixed forests can be inferred from this limitation of decomposition rate of *G. dewevrei*.

Leaf litter of *G. dewevrei* indicated an initial lag time in decomposition up to 3 months of incubation where k_{app} value reached 0.10 month^{-1} (Figure 3.2b). A slower initial decomposition rate relates to the delay in colonisation and establishment of microbial community which is reinforced by the relatively high concentrations of recalcitrant phenolic compounds [Freschet et al., 2012a; Cornwell and Weedon, 2014]. Surprisingly, no significant changes over time in decay rates of *A. mannii*, *C. hankei*, *J. seretii*, *P. oxyphylla* and *P. suaveolens* were reported although there was an appreciable slowing of decomposition over time for *S. Zenkeri* and *G. thompsonii*. Decay rate often decreases during litter decomposition due to changes in substrate composition (such as increasing lignin concentration but decreasing cellulose concentration) explained by the selective decomposition of the litter organic components by microbes [Berg and McClaugherty, 2014] and by the leaching of soluble compounds and tissues.

However, decrease in decay rate may also be a reflection of the dry season during the last 2 months of the experiment. Based on the meteorological data collected in Yangambi (100km to the west of Kisangani), high precipitations were reported in the early phase of incubation (from September to December) with a maximum of 321 mm in November but dropped below 60 mm in January and February. In addition, the decline in decay rate may also be attributed to the mesh size of litterbag limiting access to animals, especially macrofauna [Swift et al., 1979; Powers et al., 2009; Wall et al., 2008]

3.4.2 Leaf litter traits predicting decomposition rate

The LES describes strong relationships between multiple functional leaf traits and is strikingly consistent across angiosperms [Reich et al., 1997; Wright et al., 2004]. The species position along the LES is associated with different strategies for carbon gain and growth. On the right side

of the LES (Figure 3.1), *A. mannii*, *G. thompsonii*, *P. suaveolens*, and *S. zenkeri* appear to be fast-growing species that produce short-lived and structurally inexpensive leaves with a high nutrient content and a high photosynthetic rate [Wright et al., 2004; Poorter and Bongers, 2006; Osnas et al., 2013]. By contrast, the position of *C. hankei*, *G. dewevrei*, *J. seretii* and *P. oxyphylla* on the left side of the LES indicates slow-growing species that produce long-lived, low-quality leaves (nutrient poor and high lignin concentration) at high-energy costs with lower photosynthetic capacity. These two groups of species show a trade-off between fast growth - high photosynthesis and slow growth - persistent, long-lived leaves [Shipley et al., 2006].

The variation in decomposition rates during early stages of decomposition (up to 3 months of incubation) was strongly associated with chemical differences in litter quality (Figure 3.3, Figure 3.4). The position of species along the LES was the best predictor of early decomposition rates followed by the individual litter traits such as Ca, S, P, N, K, lignin and Mg concentrations or C:S, lignin:N, C:P, C:N and N:P ratios. The relation between LES and decay rate indicate that species with fast acquisitive leaf traits show higher decomposition rates than species with slow conservative traits and is consistent with previous studies [Santiago, 2007; Bakker et al., 2011].

Litter decay rate is linked to several litter traits simultaneously and each species has a unique combination of all the traits that influence litter breakdown. Therefore, it is not surprising that focusing on the position across the litter economics spectrum result in the best prediction of litter decomposability.

As expected, nutrients concentration tends to enhance litter decomposition. Strongest relationship between individual trait and decay rate was reported for Ca concentration. As important constituent of fungal cell walls and of certain arthropods exoskeleton, these decomposer organisms need high amounts of Ca in their diets [Swift et al., 1979; Reich et al., 2005; Lovett et al., 2016]. In addition, high concentrations of cations such as Ca and Mg in leaf litter make litter less acidic and therefore

making it more palatable for decomposer organisms [Cornelissen et al., 2003]. Earthworms, termites, ants and millipedes have been identified as the most important macro-invertebrates contributing to litter decomposition in tropical wet forests [Powers et al., 2009; Ewers et al., 2015].

Not surprisingly, leaf P concentration was a better predictor of litter decay rate than N concentration (R^2 of 0.47 and 0.64 for relationships between decay rates and N and P concentrations, respectively). Indeed, while N availability is an important driver of decomposition rate in temperate forests, P is the most limiting nutrient for plant growth in tropical rainforests [Vitousek, 1984; Cleveland et al., 2002]. Limitation of decomposition rates by N, S, or P is also indicated by the significant negative effect of C:N:P:S stoichiometry and lignin:N ratios on decay rates. Higher C:N, C:P, C:S, N:P and lignin:N ratios are clear indication of lower N, P and S availability inducing lower use efficiency of decomposers community [Enriquez et al., 1993; Zhang et al., 2008].

No relationships were reported between decay rates and litter Cellulose, Mn and Si concentrations. The cellulose, other major cell-wall constituents and hardly degradable, is expected to have great impact on decomposition rate in a similar way as lignin [McClaugherty and Berg, 1987]. Despite increasing evidence that Si in cell walls also plays a role in mechanical defence against fungi and herbivores [Epstein, 1994; Reynolds et al., 2009], Si was not significantly correlated to decay rate. As a cofactor of the enzyme manganese peroxidase, Mn has been shown to enhance lignin degradation [Berg et al., 2007; Keiluweit et al., 2015]. However, Cellulose, Si and Mn are known to exhibit the greatest influence in late stages of litter decomposition. Therefore, longer incubation period would be needed to detect the influence of these factors.

3.4.3 Home field advantage

Initial mass losses (during the first two months) of the dominant species (*S. zenkeri* and *G. dewevrei* in MIF and MOF, respectively) were significantly different between both forest types (Table 3.2). The litters

of the *S. zenkeri* and *G. dewevrei* showed a larger mass loss (from 4.53 to 9.17%) in their environment of origin, MIF and MOF, respectively. In a review of studies about HFA effect, Veen et al. [2015] reported a mean positive HFA effect of 5.6% which is consistent with our results. However, HFA is often associated to a large variability, indicating considerable variation in the magnitude and direction between observations. According to the home-field advantage hypothesis (HFA), leaf litter generally decomposes faster beneath the plant species from which it had been derived, owing to specialization of litter and topsoil decomposer communities to break down litter encountered most often [Ayres et al., 2009; Veen et al., 2015]. Ayres et al. [2009] and Freschet et al. [2012a] showed that HFA effect increases with greater dissimilarity in litter quality and in plant communities across sites. Given the strong contrast in species composition between MIF and MOF [Cassart et al., 2016] and in litter quality of their dominant species (Figure 3.1, Table 3.1), *S. zenkeri* and *G. dewevrei* were a good opportunity to test for the HFA under tropical forest.

By contrast, Torti et al. [2001] reported substantially lower litter mass loss for *G. dewevrei* under its own environment of origin compared to the adjacent mixed forest in the Ituri Forest (250 km east of Kisangani) and attributed this negative effect to higher mesofauna activity under the mixed forest. In Cameroon, Peh et al. [2012] observed no significant forest type effect on litter decomposition of different species including *G. dewevrei*.

3.4.4 Litter mixing effect on decomposition

Litter mixing can affect decomposition both through additive and non-additive effects (positive or negative). Our experiment assessed litter mixture effects on decomposition along litter dissimilarity gradients generated by assembling the full set of 28 pairwise species combinations that can be derived from a pool of eight species.

Similarly to the decomposition of pure litterbags, litter mass loss of mixtures after 1 and 6 months of incubation was clearly linked to the litter mixture position along the LES determined from the litter quality of the single species (Figure 3.5).

On average, litter mass losses after 1 and 6 months of incubation in mixed litterbags were respectively 3.21% ($P < 10^{-5}$) higher and 2.65% ($P = 0.06$) lower compared to predicted values calculated based on the decay rates of single species. After 6 months of incubation, no mixture decomposed faster than the fastest pure litter treatment (*G. thompsonii*) or less rapidly than the slowest single litter treatment (*G. dewevrei*). Indeed, litter mixing effects on decay rates appeared to be weak after 6 months of incubation. However, strong variation in $DERM_m$ among litter mixtures was reported (Table 3.3). For both incubation duration, the overall net outcomes were driven by a small number of observations, the great majority showing neither significantly positive nor negative $DERM_m$. In particular, only 6 pairwise species exhibited strong negative $DERM_m$ ranging from -11.97 to -17.09% after 6 months while all other mixtures ranged from -6.98 to +7.00% (Table 3.3). As shown by numerous studies, when non-additive mixing effects occur, differences between observed and predicted mass loss up to 20% are common [Hoorens et al., 2003; Gartner and Cardon, 2004; Hättenschwiler et al., 2005].

Incubation time was an important factor to capture the $DERM_m$. $DERM_m$ were not consistent over time as both antagonistic and synergistic effects occurred. Influence of incubation time (either antagonistic and synergistic) on litter mixing is consistent with previous studies [Wardle et al., 1997]. However, Lecerf et al. [2011] and Wu et al. [2013] observed inverse pattern, with antagonistic effect of litter mixture in initial stage of litter break down followed by synergistic effect. The change in $DERM_m$ over time could be accounted for by the temporal variations of microclimate, decomposer community and litter chemistry in the decomposition processes. Early phase of decomposition is mainly driven by nutrients whereas secondary compounds (e.g. lignin) influence the latter decomposition stage [Berg and McClaugherty, 2014].

71% of the variation in $DERM_m$ was explained by a combination of the chemical dissimilarity between the component species (CD_m), the decay stage (DS_m) and the maximum relative decomposition index of the mixture ($MRDI_m$) (Table 3.4), yet the individual contribution of those factors strongly differed. Significant impact of DS_m on litter decomposition is not surprising. Indeed, significant $DERM_m$ can be more easily detected if the decay of the litter is more pronounced.

One of the mechanisms behind positive litter mixture effects is the active microbial nutrient transfer from nutrient-rich to nutrient-poor litter [Gessner et al., 2010]. Fungi growing in nutrient-poor litter can redistribute limiting nutrients, such as P, by extending their hyphae to the richer litter species [Schimel and Hättenschwiler, 2007]. These mechanisms can be illustrated via the mixtures including *S. zenkeri* and *G. dewevrei*, the most abundant species in MIF and MOF, respectively. While the litter of *S. zenkeri* showed one of the highest nutrients concentration across species, the litter of *G. dewevrei* was reported as the most recalcitrant (Table 3.1, Figure 3.1). First, through an enhancement of the decomposition of its neighbour ($DERM_n$: +10%, Figure 3.6b), the mixtures including *S. zenkeri* exhibited on average the highest $DERM_m$ after 1 month of incubation (Figure 3.6). On the other hand, the decomposition of *G. dewevrei* after 1 month was improved by the presence of every neighbour (Figure 3.6c). In addition to this active translocation, passive transfers via leaching and subsequent transport by water flow of soluble nutrients and carbon compounds can occur. In addition, some recalcitrant and/or inhibitory compounds (e.g. phenolics) can also be involved in such passive transfers leading to negative effects on decomposition as observed after 6 months of incubation in this study. As shown in Figure 3.6b, the presence of *G. dewevrei* in mixture strongly decrease the decomposition of its neighbours after 6 months ($DERM_n$: -10%).

However, litter quality has been shown to change during decomposition [Parton et al., 2007; Manzoni et al., 2008] leading to a varying CD_m . Therefore, although CD_m significantly enhanced litter decomposition after both 1 and 6 months, CD_m should be estimated from litter trait of the corresponding period of measurement in order to investigate its effect

on litter decomposition during late phase. Though significant, its effect is strongly weaker compared to DS_m and $MRDI_m$ effects (Figure 3.7). Doubling CD_m only enhance litter decomposition of mixture of 22 and 25% after 1 and 6 months of incubation respectively.

$MRDI_m$ impact on decomposition strongly differed with time (Table 3.4). When DS_m and CD_m were kept constant, doubling the value of $MRDI_m$ lead to a decrease of 35 and 117% in $DERM_m$ after 1 and 6 months, respectively. After 6 months of incubation, strongest negative $DERM_m$ was shown by mixtures including *S. zenkeri*, *G. thompsonii* and *P. suaveolens* which exhibited the highest initial decay rate in pure condition (Figure 3.2, Figure 3.6) Therefore, the highest $MRDI_m$ were reported for mixtures including these 3 easily decomposable species (see Appendix 14 for $MRDI_m$ by mixture type). The great negative $MRDI_m$ effect reported suggesting that presence of easily decomposable litter species in the mixture substantially reduce its decomposition. These strongly negative $DERM_m$ were mainly due to the decreasing in litter mass loss of these 3 readily decomposable species for which $DERM_t$ ranged from -8.61 to -25.23% (Figure 3.6c). The transfer of inhibitory compounds from the most recalcitrant litter in the mixture can suppress the decomposition rate of its neighbour [Gartner and Cardon, 2004; Hättenschwiler et al., 2005].

Strong individual species identity effects were observed. Indeed, considering mixture as a whole may mask species-specific responses to mixing litter that might be important for decomposition processes. Certain additive effects ($DERM_m$ not significantly different from 0) reported in this study mask contrasted $DERM_t$ and $DERM_n$. As an example, *C. hankei* significantly decreased the decomposition of its neighbours ($DERM_n < 0$) while its own litter mass loss was enhanced ($DERM_t > 0$) by mixing leading to the absence of effect on whole mixture after 6 months (Figure 3.6b and 3.6c). Conversely, with *J. seretii* litter, the null $DERM_m$ reflect a true additive effect. Indeed, after 6 months of incubation, the individual decomposition of the *J. seretii* was not affected by mixing (Figure 3.6c) and the presence of *J. seretii* appeared to not influence in average the litter mass loss of its neighbours (Figure 3.6b).

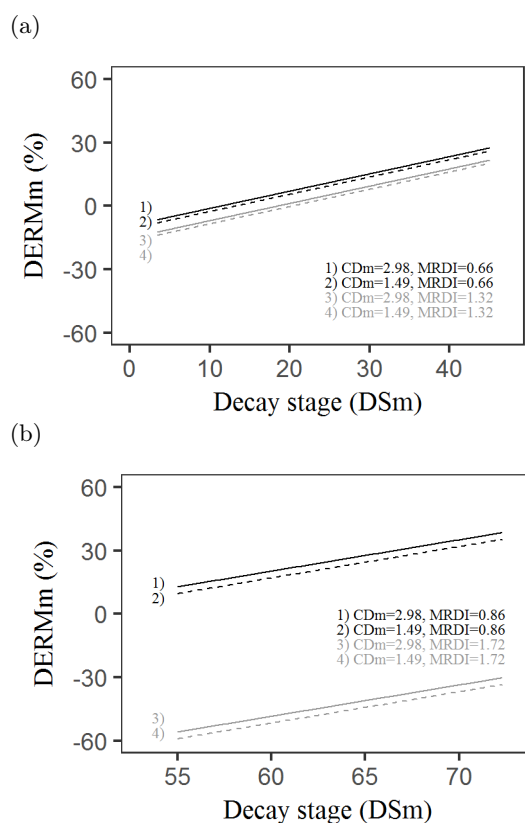


Figure 3.7 – Illustration of model predictions of DERM_m (see Table 3.4) after 1 (a) and 6 (b) months of incubation in function of decay stage of the mixture (DS_m) estimated by keeping constant the chemical dissimilarity (CD_m) and the MRDI_m at two levels; (i) minimum reported for the variable and (ii) its double. Different line types with similar colour represent the effect on DERM_m of change in CD_m with constant MRDI_m whereas similar line type with different colours represent the effect of change in MRDI_m with constant CD_m

DERM_t and DERM_n exhibited higher range compared to DERM_m, especially after 6 months of incubation (Figure 3.6). However these greater non-additive effects masked yet important contrasted individual behaviour in a same mixture. In average, *G. dewevrei* decreased the litter mass loss of its neighbours by 10% from the expected values in pure litterbags after 6 months (Figure 3.6b). Nevertheless, the presence of *G. dewevrei* had little impact on the decay rates for five of the eight species involved in the experiment but strongly affected the litter mass loss of the two easily decomposable species; *S. zenkeri* and *G. thompsonii* exhibited mean DERM_n of -43.43 and -27.18% in presence of *G. dewevrei* (see Appendix 15). On the other hand, the presence of *J. seretii* in mixture did not appear to affect the decomposition rate of its neighbours after 6 months of incubation (DERM_n: -0.04%, Figure 3.6b). However, both strong negative and positive effects were reported with a DERM_n of -23.39 and +17.73% for *S. zenkeri* and *A. mannii* as neighbour of *J. seretii* (see Appendix 16) leading to an average "no effect" (Figure 3.6b).

3.5 Conclusions

As expected, combining all studied litter traits in a "leaf economics spectrum" (LES) through a PCA analysis allowed an improved prediction of the individual decay rates of the 8 species involved in the decomposition experiment in pure litterbag compared to each traits individually. The contrasted leaf litter functional traits of the two dominant species (*S. zenkeri* and *G. dewevrei* for MIF and MOF, respectively) lead to strongly different decay rates which is in agreement with the greatest organic matter accumulation in mineral soil and forest floor under MOF [Cassart et al., 2016]. Moreover, we showed that both *S. zenkeri* and *G. dewevrei* exhibited more favourable decay rate under their own forest types, in agreement with the "home field advantage" (HFA).

Our results showed that there was a weak but significant effect of litter mixing on decomposition suggesting a form of stabilisation of the decomposition rate in mixture through complex interactions among component

species. Furthermore, by separating component species of the mixture, we have highlighted that these weak mixing effects may mask strongly contrasted situations. The results of our DERM model emphasize that species identity in interaction with the decay stage of the mixture were important for determining the mixture effect on the decomposition rate. Contrary to expectations, we showed that the difference in initial litter quality across component species was not useful to explain interactions in litter mixture.

Chapter 4

Functional traits drive the difference in
soil respiration and its partitioning
between *Gilbertiodendron dewevrei*
monodominant forests and
Scorodophloeus zenkeri mixed forests in
the Central Congo basin

Abstract

In tropical rainforests, soil respiration accounts for the major part of total ecosystem respiration, yet a mechanistic understanding of the influence of forest type and species composition is still lacking. To that end, daily soil respiration with and without forest floor contribution was measured monthly during a one-year period in two emblematic rainforest types of the Central Congo basin: the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). Through a process-based conceptual model parameterized by environmental variables collected under MIF and MOF (soil moisture and temperature, soil organic C stocks and fine roots biomass), we investigated the drivers behind the difference in total (R_T), autotrophic (R_A) and heterotrophic (R_H) soil respiration between forests. Compared to a semi-empirical model involving only soil temperature and moisture, the conceptual model provided a better understanding of temporal and spatial variation in soil respiration. On an annual basis, R_T was 10% higher under MOF ($22.10 \text{ Mg C ha}^{-1} \text{ y}^{-1}$) compared to MIF ($20.01 \text{ Mg C ha}^{-1} \text{ y}^{-1}$) ($P < 10^{-3}$) and forest floor removal ($O_L + O_F + O_H$ layers) significantly reduced R_T only in MIF, by *ca.* 18%. While R_A and R_H contributed about equally to R_T in MOF, R_A slightly dominated (59%) in MIF. Model simulations showed that the increased R_H was related to the twofold C accumulation in MOF topsoil compared to MIF. Volumetric soil water content was a major driver of temporal changes in soil respiration, but hardly impacted the differences in annual soil respiration between forests. Through their effect on organic matter decomposition, low nutrient to C ratios of *Gilbertiodendron dewevrei* tissues strongly impacted soil C dynamics under MOF.

4.1 Introduction

In the context of increasing CO₂ concentration in the atmosphere and associated climate change, understanding biophysical controls on carbon (C) fluxes and stocks in terrestrial ecosystems is of major importance. C sequestration in forest ecosystems is the result of a delicate balance between uptake (photosynthetic carbon fixation) and loss (ecosystem respiration) [Malhi et al., 1999; Chen et al., 2013]. In tropical forests, soil respiration (R_T) accounts for more than 70% of total ecosystem respiration [Malhi et al., 1999]. In addition, tropical forests have the highest soil respiration rates globally [Raich and Schlesinger, 1992; Luyssaert et al., 2007; Hashimoto et al., 2015]. Despite their key role in the global C cycle, the tropical forests have been less studied and their C budget, sources vs. sinks of carbon, is still controversial [Clark, 2004].

R_T results from the activity of roots and the associated rhizosphere (autotrophic component, R_A) and from the decomposition of organic materials from aboveground and belowground litter by micro-organisms (heterotrophic component, R_H) [Hanson et al., 2000; Subke et al., 2006]. Both autotrophic and heterotrophic soil respirations involve various biological and ecological processes and are highly variable at all spatial (from respiration chamber to forest stand) and temporal (hours to years) scales. Therefore, their response to change in environmental conditions may differ [Subke et al., 2006; Epron, 2009]. However, contrasting results reported in numerous studies in tropical forests highlight the poor mechanistic understanding of this process [Holland et al., 2000; Wei et al., 2010; Melillo et al., 2011; Cavaleri et al., 2015].

In tropical rainforests, soil moisture and, to a lesser extent, soil temperature are recognized as the most influential environmental factors controlling variation in R_T [Davidson et al., 2000; Hall et al., 2013; Tan et al., 2013; Wood et al., 2013]. Besides these two main environmental drivers, the size of the soil organic C (SOC) pool, the quality of organic matter inputs (above and belowground), the abundance of roots and the distance and the size of the surrounding trees have been shown

to strongly affect R_T and its components (R_A and R_H) [Epron et al., 2004; Pregitzer and Euskirchen, 2004; Wang et al., 2010; Bréchet et al., 2011; Hopkins et al., 2013]. Since all these variables are influenced by the forest cover [De Deyn et al., 2008], R_T and its components should be largely impacted by forest composition.

Tree species identity impact on R_T is linked to functional traits that drive C assimilation, transfer and decomposition through the activity of autotrophs and heterotrophs, as well as through the modification of abiotic conditions [De Deyn et al., 2008]. Indeed, tree species might affect soil CO_2 efflux through a variety of mechanisms, mainly by controlling the quantity and the quality of aboveground and belowground litter production in one hand, and root-derived respiration (root respiration and root exudates) on the other hand [Metcalf et al., 2011].

R_H is the product of the microbial decomposition of soil organic matter and is directly affected by litter quantity and quality (e.g. C:N ratio, lignin and nutrient concentrations), via the alteration of the microbial communities and the decomposition rates [Keller et al., 2013; Bréchet et al., 2017]. Higher litter inputs correspond to potential greater availability of labile C components and nutrients and thus to increased OM decomposition [Liu et al., 2009].

R_A originates from the growth and the activity of the tree roots. Although coarse roots ($> 2\text{mm}$) are the most important contributor to root biomass, variability in R_A has been shown to be mainly explained by changes in fine roots ($\leq 2\text{mm}$) biomass [Hopkins et al., 2013]. Changes in temperature lead to changes in plant C assimilation, belowground C allocation and root growth and therefore impact R_A . Aside from promoting R_H by increasing decomposition rate of OM, an increase in N availability may enhance tissue N concentration, resulting in increasing associated protein maintenance and construction costs that stimulate R_A [Wang et al., 2010; Hopkins et al., 2013]. However, all these factors affecting both R_A and R_H do not act independently, may interact with each other and mutually affect soil respiration.

Forest floor organic layer provide an major source of C for soil respiration and also contribute to a microclimate that favours the activity of decomposer [Luo and Zhou, 2006]. Through resource limitation, forest floor removal has often been shown to substantially reduce total soil respiration by up to 40% in tropical forests [Vasconcelos et al., 2004; Sayer et al., 2007]. However, despite the major role of the forest floor decomposition to nutrient and C cycle in tropical rainforest, the influence of forest type and species composition behind the variability in the litter layers contribution to R_T remain poorly studied.

Tropical rainforests comprise a large range of tree species composition and diversity, from highly diverse forest with up to 300 tree species per ha [Sullivan et al., 2017] to ecosystems where nearly one single tree species dominates in the upper canopy layer [Connell and Lowman, 1989; Peh et al., 2011a; Brookshire and Thomas, 2013; Kazmierczak et al., 2016]. Whereas such contrasts in species composition and diversity may potentially lead to substantial changes in R_T and its components [Raich and Tufekciogul, 2000; Bréchet et al., 2009; Metcalfe et al., 2011; Guo et al., 2016], the influence of forest type on R_T remains largely unknown.

Here we investigate R_T in two emblematic forest types of the Central Congo basin, in DR Congo: the *Scorodophloeus zenkeri* Harms mixed forests (MIF) and the evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF). These two forest types cover extensive areas in the zone, where they frequently co-occur on similar ecological conditions [Hart et al., 1989; Cassart et al., 2016; Kearsley et al., 2017]. The specific objectives of this paper were: (i) to estimate the contribution of the forest floor to total soil respiration; (ii) to quantify the autotrophic (R_A) and heterotrophic components (R_H) of R_T ; (iii) and to investigate the drivers behind the spatial and temporal variation of R_T and its components for the two forest types.

To that end, we measured R_T monthly with and without the forest floor during a one-year period in MIF and MOF, and parameterized a process-based conceptual model that separates R_T into R_A and R_H components using measured environmental variables; soil organic C stocks (forest

floor and 0-10cm mineral soil layer), pedoclimatic variables (soil temperature and moisture) and fine roots biomass.

4.2 Materials and methods

4.2.1 Site description

Our investigations were carried out in 2012 and 2013 in the Yoko Forest Reserve in the Tshopo province (Democratic Republic of Congo, DRC). The reserve is located on a sandy plateau at about 28 km south of Kisangani (00° 19'12" N, 25° 17'43" E; 450 m above sea level) and covers an area of 6975 ha. Vegetation within the reserve consists of pristine moist semi-deciduous rainforest mixed with variable patches of moist evergreen rainforests. Few transition forests and slash-and-burn agriculture areas are found on the west side of the reserve, along the road.

Based on the meteorological data collected from the Yangambi station (located 100 km to the west of Kisangani) between 1961 and 2009, the annual precipitation averages 1780 (± 230) mm with two distinct rainy seasons (March-June and August-December), and a cumulated dry season length of *ca* 3 months (January-February and July) with monthly precipitation lower than 60 mm. The mean annual air temperature is 24.8°C with minimal variation across the year. The dominant soil type is classified as Xanthic Ferralsol [Van Ranst et al., 2010; WRB, 2014] mostly composed of quartz sand, with low content of kaolinite clay and hydrated iron oxides.

A preliminary survey allowed us to select areas of the Reserve dominated either by semi-deciduous *Scorodophloeus zenkeri* Harms mixed forests (MIF) or by evergreen *Gilbertiodendron dewevrei* (De Wild.) J.Léonard monodominant forests (MOF), in otherwise similar climatic, topographic and edaphic conditions. As reported by Cassart et al. [2016] the soils under MIF and MOF had similar chemical and physical soil properties. They were highly weathered and acidic ($\text{pH} < 4.8$), with a coarse sandy texture that slightly decreased with depth (see chapter 2).

As shown in Table 4.1, the dendrometric characteristics were not significantly different between the two forest types while species composition and diversity strongly differed. Species diversity quantified by the Shannon Diversity Index was much higher in MIF compared to MOF. While *S. zenkeri* accounted for 28.2% of the total basal area (BA) in MIF, the contribution of *G. dewevrei* to total BA accounted for 73.1% in MOF allowing this forest to be classified as monodominant [Connell and Lowman, 1989]. Additional information on site and stand characteristics may be found in Cassart et al. [2016].

4.2.2 Measurements and sampling

Sampling zone

One hundred and six 40-m x 40-m plots were established (77 and 29 in MIF and MOF, respectively) within an area of 2 km². Based on the higher species diversity under MIF compared to MOF, we expected a higher variability of R_T in MIF. Therefore, we installed a higher number of plots in MIF. Each plot was centred on a tree cluster which comprised three mature trees of the canopy layer forming a triangle with the trees ranging 2.5-9.3 m from the centre of the cluster (Figure 4.1c). Four types of clusters were chosen for investigation: monospecific clusters (each cluster tree belongs to the corresponding dominant tree species, ie *S. zenkeri* and *G. dewevrei* in MIF and MOF, respectively), two-species clusters including the dominant tree species, three-species clusters including the dominant tree species and three-species clusters without the dominant tree species (see Appendix 17 for the distribution of the 106 plots between these four types of cluster). Because of its lower species diversity (Table 4.1), only mono- and two-species clusters were established in MOF. In each plot, all living trees with a DBH > 10 cm were measured and identified to species level, and all trees with DBH > 16 cm were mapped to determine local stand characteristics.

Table 4.1 – Summary of forest, soil and fine roots (FR) characteristics for the mixed (MIF) and monodominant (MOF) forests (averages $\pm$ standard deviations). Five most abundant species based on their basal area ratio (%). Species abbreviations for *Scorodophloeus zenkeri*, *Cynometra hankei*, *Julbernardia seretii*, *Prioria oxyphylla*, *Tessmannia africana*, *Gilbertiodendron dewevrei*, *Cola griseiflora*, *Panda oleosa*. Different letters in a row indicate significant difference between forests ($P \leq 0.05$). Stand characteristics and species diversity were derived from stand inventories as described by Cassart et al. [2016]

	MIF	MOF
Forest characteristics		
Stand density (tree.ha ⁻¹)	392 $\pm$ 13 ^a	405 $\pm$ 28 ^a
BA (m ² .ha ⁻¹)	31.4 $\pm$ 2.7 ^a	34.9 $\pm$ 6.5 ^a
Species diversity		
Shannon index	3.12 $\pm$ 0.04 ^a	1.49 $\pm$ 0.01 ^b
Most abundant species	<i>S. zenkeri</i> (28.2%)	<i>G. dewevrei</i> (73.1%)
	<i>C. hankei</i> (7.0%)	<i>S. zenkeri</i> (7.8%)
	<i>J. seretii</i> (4.7%)	<i>P. oxyphylla</i> (6.0%)
	<i>P. oxyphylla</i> (4.6%)	<i>C. griseiflora</i> (1.8%)
	<i>T. africana</i> (3.0%)	<i>P. oleosa</i> (1.6%)
Soil climate (0-10 MS layer)		
SVWC (m ³ m ⁻³)	0.33 $\pm$ 0.12 ^a	0.38 $\pm$ 0.13 ^b
Temperature (°C)	23.64 $\pm$ 0.62 ^a	23.78 $\pm$ 0.53 ^b
SOC stocks (Mg C ha⁻¹)		
0-10 MS layer	13.62 $\pm$ 2.80 ^a	22.24 $\pm$ 6.08 ^b
O _L	1.13 $\pm$ 0.45 ^a	2.85 $\pm$ 1.09 ^b
O _F +O _H	1.43 $\pm$ 0.75 ^a	3.83 $\pm$ 1.88 ^b
Fine roots		
FR biomass in FF (Mg ha ⁻¹)	0.81 $\pm$ 0.20 ^a	0.79 $\pm$ 0.20 ^a
FR biomass in MS (Mg ha ⁻¹)	1.93 $\pm$ 0.64 ^a	1.80 $\pm$ 0.59 ^b

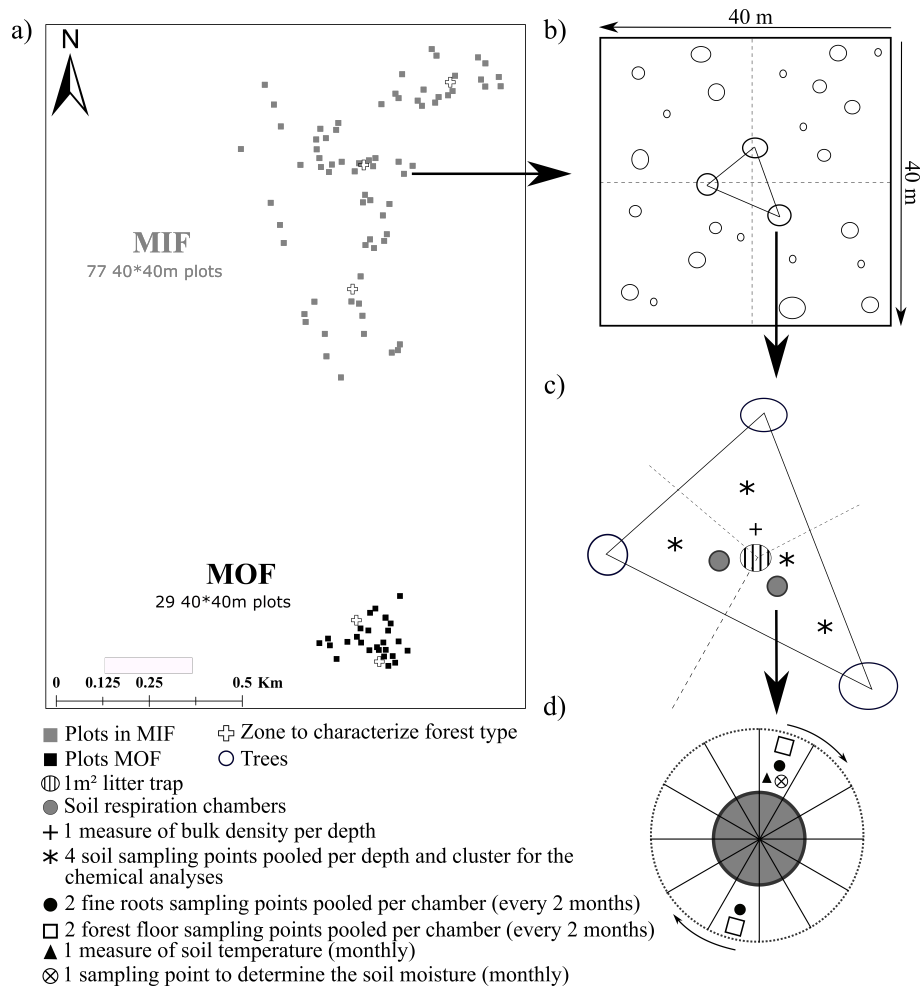


Figure 4.1 – Sampling plan and sampled locations in MIF and MOF. a) Study area, indicating the location of the plots and pits in MIF and MOF. b) Configuration of the cluster within the plot. c) Measurement of soil respiration and sampling of litterfall, mineral soil and soil bulk density within a cluster area. d) Sketch showing the shift in sampling/measurement location for soil temperature, soil moisture, fine roots and forest floor around the chamber over time during the study period

Measurements of litterfall, soil respiration, temperature and water content

Within each plot, 1-m² circular litter traps (1.3 m high) were installed in the centre of the cluster (Figure 4.1c) and litterfall was collected monthly from May 2012 to April 2013. Coarse woody debris with a diameter > 1 cm were discarded and the remaining litter was sorted into two fractions (leaves and fine woody debris). All litterfall components were dried at 70°C during 48-h and weighed. Annual leaves and fine woody debris litterfall (AL_L and AL_W) were calculated by summing up the monthly C inputs. C and N analyses were performed by the dry combustion method (Thermo Finnigan Flash EA 1112 elemental analyser) on composite litterfall samples of each litterfall fractions pooled over three months (May to July, Aug. to Oct., Nov. to Jan. and Feb. to April).

In addition, total daily soil respiration (R_T) was measured monthly from May 2012 to April 2013 using the soda lime technique as described in Keith and Wong [2006] in each plot. The measurements were conducted at the same locations during the study year. Briefly, CO₂ emitted from the soil was absorbed for 24 h in 60 g of predried soda lime granules in inert glass petri dish placed on wire stands suspended above the litter surface to avoid obstructing CO₂ efflux from the soil. The chambers consisted of white polyethylene plastic buckets with the base cut off (25 cm tall, 30 cm diameter and inserted 3 cm in the soil 4 weeks prior to the start of the measurements) and a heavy lid that adequately sealed the chamber during measurement. Every chamber was kept free of seedlings and woody debris throughout the whole measurement period. Four blanks per forest type were used to account for CO₂ absorption during handling and drying.

In order to assess the forest floor (FF) contribution to soil respiration, a second respiration chamber was set up in each monospecific cluster (n=16 and n=13 in MIF and MOF, respectively; Appendix 17). In each of these chambers, four weeks prior to the start of soil respiration measurement, litter layer was removed without damaging the superficial root mat, placed on a removable device made from metal mesh and reinstalled in the respiration chamber. This apparatus allowed us to

measure soil respiration monthly from May 2012 through April 2013 without FF contribution (R_{WF}) by removing the litter layer only during the measurement day while keeping it during the rest of the period. Litter contribution can be estimated by subtracting CO_2 efflux in the chamber with periodic litter removal from the respiration in the control chamber.

The soil temperature at 5 cm depth was simultaneously monitored adjacent to each chamber just after respiration measurement using a digital thermometer. Soil moisture (volumetric water content, SVWC) was determined on two 0-10 cm deep soil cores ($2 \times 100 \text{ cm}^3$) in undisturbed areas directly adjacent to the chamber immediately after CO_2 measurement; soil samples were weighed and oven-dried at 105°C for 48-h. Due to important power supply issues during the oven drying of the soil samples, SVWC is only available from July 2012.

Forest floor, fine roots and soil sampling

FF was sampled every two months from May 2012 to March 2013 in two opposite selected points around each chamber (cf. Figure 4.1d), using a 20×20 cm metal frame. For each sample, the litter component (O_L) and the decomposed organic matter ($O_F + O_H$) were separated. Briefly, O_L was described as non-decomposed fallen plant material and $O_F + O_H$ as partly or strongly decomposed organic material (see van Delft et al. [2006]). Samples were then pooled per respiration chamber for determination of oven-dry mass (70°C during 48-h). Samples from July were grinded for C and N analyses.

Fine roots (FR; roots ≤ 2 mm in diameter) were sampled every two months from July 2012 to March 2013 from the upper 0–10 cm mineral soil (MS) layer in two opposite selected points around each respiration chamber (cf. Figure 4.1), using Kopecky cylinders (250 cm^3). Roots were removed from the soil by wet sieving and separated into fine (≤ 2 mm) and coarse roots using a vernier scale. Samples were then pooled per respiration chamber for determination of oven-dry mass (70°C during 48-h).

MS samples (0-10 cm depth) were collected in May 2012 at four locations per cluster, using an Edelman auger sand-type. No coarse fragments were found in mineral soil samples; similarly, we did not detect any charcoal presence. Samples were then pooled into one sample per cluster, air-dried, sieved at 2-mm and milled for C and N analyses. Bulk densities were determined at one location per plot, using Kopecky cylinders (100 cm³) after sieving at 2-mm and oven-drying at 105°C. Soil pH was determined potentiometrically in 0.01 M CaCl₂ (1:5 soil:solution ratio).

In order to assess decay rate of MS, we carried out a laboratory incubation experiment. MS soil samples from monospecific and 2-species plots (n=36 and 29 respectively in MIF and MOF) were sieved at 2-mm and moistened at field capacity with deionized. The soil samples (30g equivalent dry soil) were then incubated during 91 days in 500-ml hermetic plastic jars containing a 30-ml vial filled with NaOH solution. The CO₂ trapped in NaOH solution was determined every week by measuring the changes in electrical conductivity according to the method of Rodella and Saboya [1999]. Experiment was conducted in duplicate per plot in a temperature-controlled dark room at 20°C. Six blanks were used to account for CO₂ absorption during handling. The water content was kept at field capacity by weighing and spraying deionized water at the soil surface during conductivity measurements, so that soil moisture did not limit microbial activity. Prior to incubation, subsamples were taken and milled for C analyses. Cumulated decay rates of MS from incubation (k_{inc} , gC-CO₂ gC_{MS}⁻¹ day⁻¹) were calculated by dividing the amount of C-CO₂ absorbed by NaOH solution by the C stocks of the incubated sample and by the corresponding number of days.

4.2.3 Conceptual model

Our conceptual model is a process-based model that simulates production of CO₂ in soil (FF plus MS). In the model, the total soil CO₂ efflux (R_T , g C day⁻¹ m⁻²) is the result of the growth and maintenance respiration of roots (R_A) and microbial respiration from organic matter

decomposition (R_H) :

$$R_T = \sum_{i=1}^3 R_{H_i} + \sum_{i=1}^2 R_{A_i} \quad (4.1)$$

The heterotrophic respiration is related to OM decomposition which is proportional to the amount of C in soil pool (SOC_i , g C m⁻²). In this model, the soil is divided into three layers assumed to exhibit contrasted maximum decay rates ($k_{i,F}$, day⁻¹): O_L , O_F+O_H and 0-10 cm MS layer. For each considered pool, maximum decay rate is constrained using soil temperature at 5 cm depth (T , °C) and its maximum (T_{max}), and soil volumetric water content ($SVWC$, m³ m⁻³) as described by Eq. 4.2 where Q_{10} is the rate of change in respiration for a 10°C increase in soil temperature. Q_{10} was fixed at 1.8, value minimizing the AIC of the model, which is consistent with the range reported for tropical forests [Hashimoto et al., 2015; Zhou et al., 2009]. Cassart et al. [2016] highlighted strong differences in the quality of organic matter inputs between MIF and MOF leading to contrasted carbon accumulation; therefore, we allowed the coefficient k to vary by forest type.

$$R_{H_i} = k_{F,i} \times SOC_i \times \sqrt{SVWC} \times Q_{10}^{(T-T_{max})/10} \quad (4.2)$$

As shown by Eq. 4.3, growth and maintenance respiration of roots (R_A) is modelled as a function of the mass of root tissue (B , g m⁻²) and the maximum specific respiration rates of roots (α , gC-CO₂ g⁻¹ day⁻¹) regulated by T and $SVWC$, similarly to R_H (see Eq. 4.2). In this study we focus on the fine roots (≤ 2 mm) biomass, the the strongest contributing pool to R_A while coarse roots represent the largest proportion of root mass [Raich and Nadelhoffer, 1989; Makita et al., 2012]. Higher fine roots productivity was reported in the FF compared to MS under tropical forests [John, 1983; Cuevas and Medina, 1988]. Therefore, in this model, fine roots biomass is divided between FF and MS.

$$R_{A_i} = \alpha_i \times B_i \times \sqrt{SVWC} \times Q_{10}^{(T-T_{max})/10} \quad (4.3)$$

In order to validate the maximum decay rate of the 0-10 cm MS layer and the fine root respiration rate obtained from the conceptual model, Equations 4.1, 4.2 and 4.3 were also fitted to the R_{WF} but without the heterotrophic components related to the FF (O_L and O_F+O_H).

This conceptual respiration model was fitted using a weighted mixed procedure with the plot and the date of measurement both nested in forest type as random effects. Residuals were weighted by a power function of SVWC to account for heteroscedasticity. The type of clusters was considered as random effect but explained no significant additional variation in R_T . We assumed that MS C stocks and the C concentrations of O_L , and O_F+O_H and MS remained constant during the respiration measurements. The B and FF C stocks not measured in August, October, December and February, were estimated based on measurements made in adjacent dates. The validity of the conceptual model was assessed by comparing the annual respiration rates predicted from our conceptual model with the observed annual respiration rates (AR_T , see section 4.2.4). Based on the conceptual model estimates, the forest floor contribution to annual R_T was obtained by summing the CO_2 efflux of both O_L and O_F+O_H derived from Eq. 4.2.

We performed a one-at-a-time sensitivity analysis of the conceptual model in order to determine whether difference in AR_T (AR_A and AR_H) between forest types is caused by input variables (SVWC, T, FR biomass and SOC stocks) and/or by model parameters (related to difference in k) [Hamby, 1994; Cariboni et al., 2007]. The method consists in repeatedly modifying one variable at a time while keeping the others fixed (e.g. to the average). To do so, three virtual "mean plots" (MP_{MIF} , MP_{MOF} and MP_T , respectively for MIF, MOF and for MIF and MOF together) were reconstructed by averaging each variable per measurement date across all the corresponding set of clusters. The difference between forest types to be used as reference was calculated by applying the conceptual model to MP_{MIF} and MP_{MOF} , estimating annual CO_2 efflux per forest and calculating the difference between MIF and MOF. The difference between forest types due to the i^{th} variable was calculated by applying the mechanistic model using the MP_T data set except for the i^{th} variable

for which values specific to each forest type (ie MP_{MIF} and MP_{MOF}) was used. This difference between forests obtained for the i^{th} variable was then divided by the reference difference to obtain an estimate of its relative contribution. A positive relative contribution of 100% indicate that difference in the i^{th} variable between MIF and MOF results in a difference in AR_A or AR_H between forest types similar to the reference difference. A negative relative contribution indicate that the difference in the considered variable between MIF and MOF tend to compensate the reference difference in AR_A or AR_H between forest types.

4.2.4 Calculations and statistical analysis

Daily respiration analysis

In order to assess the impact of separating the contributions of R_A and R_H in modelling R_T , the conceptual model was compared to the semi-empirical model given by equation 4.4. This model was also fitted using a weighted mixed procedure with the plot and the date of measurement nested within forest type as random effects. Residuals were weighted by a power function of SVWC to account for heteroscedasticity.

$$R_T = a_F + b_F \times \sqrt{SVWC} \times Q_{10}^{(T-T_{max})/10} \quad (4.4)$$

where a_F and b_F are forest type dependent coefficients.

Annual respiration analysis

Using the daily respiration data (R_T or R_{WF}) measured monthly from May 2012 to April 2013, annual soil CO_2 efflux (AR_T or AR_{WF} , $Mg\ C\ ha^{-1}\ year^{-1}$) were estimated with equation 4.5, where $R_{T/WF,m}$ is the m-month daily soil respiration and D_m the number of days of the m-month.

$$AR_{T/WF} = \frac{\sum_{i=1}^{12} R_{T/WF,m} \times D_m}{100} \quad (4.5)$$

AR_A and AR_H were estimated similarly from R_A and R_H predicted by the conceptual model.

In order to explore the possible drivers behind the spatial variability of AR_T across forest types, we used linear regression with a backward and forward selection procedure based on the Akaike Information Criterion (AIC) using a set of explanatory variables. These variables were classified into the following four categories: (i) leaf litter quantity (AL_L), (ii) fine root production, (iii) stand parameters (forest type, total basal area (BA) and weighted BA (BA_W), and distance to the nearest tree) and (iv) soil parameters (C:N ratios, C and N stocks in both MS and FF, pH of the 0-10 cm MS layer). Fine root production in FF (FRP_{FF}) and in MS (FRP_{MS}) was calculated with the Maximum-Minimum formula described by Brunner et al. [2013]. For BA_W , each trunk cross section (S_i) was weighted by the ratio between the distance of the tree from the cluster centre (r_i) and its DBH according to eq. 4.6:

$$BA_W = \frac{\sum_{i=1}^n S_i \times (1 - (\frac{r_i}{DBH_i})^2)}{\pi \times 20^2} \quad (4.6)$$

Statistical analysis

Paired t -tests were used to assess differences between R_T and R_{WF} at both daily and annual scales. Annual forest floor contribution to soil respiration was calculated by averaging the paired differences ($AR_T - AR_{WF}$) and was compared against zero using a t -test. Before performing statistical analyses, the normality of all variables was tested by skewness and kurtosis normality test. All statistical analyses were performed in R version 3.2.2.

4.3 Results

4.3.1 Environmental variables

On average, the difference in SVWC between forest types during the measurement period (0.33 ± 0.12 and $0.38 \pm 0.13 \text{ m}^3 \text{ m}^{-3}$ in MIF and MOF, respectively) did not exceed 13% (Table 4.1). SVWC displayed a strong seasonal trend (Figure 4.2a). In both forests, SVWC values peaked during both rainy seasons; Oct-Dec and Mar-Apr (Figure 4.2a). However, the increase started a month earlier in MIF and the maximum SVWC during the main wet season was almost 50% lower in MIF ($0.33 \pm 0.06 \text{ m}^3 \text{ m}^{-3}$) compared to MOF ($0.46 \pm 0.06 \text{ m}^3 \text{ m}^{-3}$). The average difference in soil temperature between MIF and MOF was lower than 1% (mean soil T: 23.64 ± 0.62 and $23.78 \pm 0.53^\circ\text{C}$ in MIF and MOF, respectively). Despite a weak increase in February, no clear seasonal variation in soil temperature was observed in any of the forest types (Figure 4.2b).

As shown in Table 4.2, annual foliar litterfall did not significantly differ between MIF ($2.86 \pm 0.49 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) and MOF ($2.79 \pm 0.44 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Monthly leaf litterfall showed two peaks of production (Figure 4.2c): in January-February (long dry season) on the one hand, and from August to September on the other (main rainy season with strong winds). Similarly, annual fine woody debris litterfall was comparable in both forest types (1.75 ± 0.48 and $1.80 \pm 0.66 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in MIF and MOF, respectively) and accounted for less than 40% of total annual litterfall (leaves + fine woody debris).

MIF exhibited higher FR biomass in MS compared to MOF (1.93 ± 0.64 and $1.80 \pm 0.59 \text{ Mg ha}^{-1}$ in MIF and MOF, respectively). In addition, FR N concentration in MS reported in MIF ($1.84 \pm 0.43 \%$) was almost twice compared to MOF ($0.97 \pm 0.35 \%$). Similar FR biomass in FF were reported in MIF ($0.81 \pm 0.20 \text{ Mg ha}^{-1}$) and MOF ($0.79 \pm 0.20 \text{ Mg ha}^{-1}$). FR biomass in FF and MS exhibited slight increases in November, following the highest monthly precipitation (Figure 4.2d). Whereas FR biomass in FF did not differ significantly between forest types, highest annual FR production in FF was observed under MOF (0.55 ± 0.19 and 0.66 ± 0.31

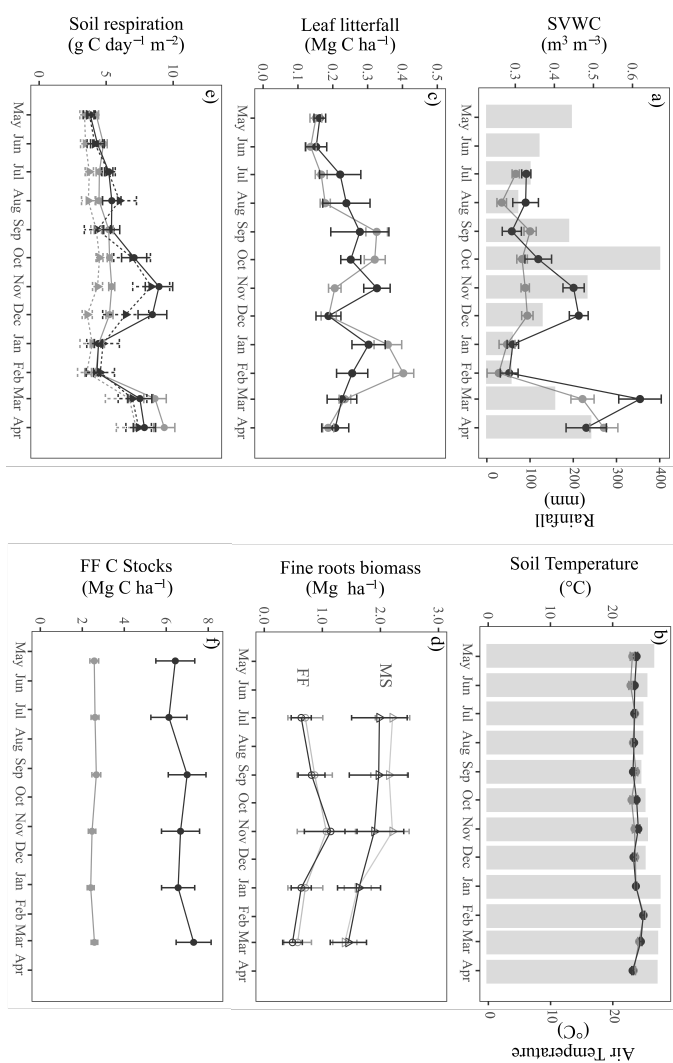


Figure 4.2 – Annual course of a) monthly precipitation (mm, gray bars) and volumetric water content of the 0–10 cm soil layer ($\text{m}^3 \text{m}^{-3}$), b) air (gray bars) and soil temperature in the 0–10 cm layer ($^{\circ}\text{C}$), c) monthly leaf litterfall (Mg C ha^{-1}), d) fine roots biomass in the 0–10 cm soil layer (white triangle) and in the FF (white circle) (Mg ha^{-1}), e) soil respiration ($\text{g C day}^{-1} \text{m}^{-2}$) with (black circle) and without forest floor contribution (black triangle) and f) forest floor C stocks (Mg C ha^{-1}) measured from May 2012 to April 2013 in the mixed (MF, in grey) and monodominant (MOF, in black) forests (averages $\pm$ standard errors)

in MIF and MOF, respectively). For both MIF and MOF, FR biomass in MS was two times higher compared to FF (Table 4.1, Figure 4.2d) in contrast to annual FR production which is highest in FF (Table 4.2).

The SOC stock in the FF plus the 0-10 cm MS layer was significantly higher under MOF (28.83 ± 6.22 Mg C ha⁻¹) compared to MIF (16.22 ± 2.81 Mg C ha⁻¹). However, this difference between forest types was higher in the FF (62%) compared to the upper MS (39%) (Table 4.1). As shown in Figure 4.2f and Table 4.1, FF C stocks were about three times higher in MOF (6.68 ± 2.29 Mg C ha⁻¹) compared to MIF (2.55 ± 0.81 Mg C ha⁻¹); O_L layer accounted for 45% of the total litter layer in both forest types. Related to peaks in monthly litterfall, FF under MOF exhibited slight increases in October and March. Nevertheless, these increases were not observed under MIF.

4.3.2 Soil respiration

On average, R_T was slightly but significantly ($p < 10^{-5}$) higher in MOF (6.08 ± 2.51 g C m⁻² day⁻¹) compared to MIF (5.48 ± 2.47 g C m⁻² day⁻¹). Similarly to SVWC, R_T exhibited strong increases in rainy seasons (Figure 4.2e) and the maximum of R_T during the main wet season in MIF (5.40 ± 0.87 g C m⁻² day⁻¹) was almost twice lower compared to MOF (9.80 ± 2.96 g C m⁻² day⁻¹). In MIF, the R_{WF} (4.37 ± 19.1 g C m⁻² day⁻¹) was 13.3% lower on average than R_T (5.32 ± 2.44 g C m⁻² day⁻¹). In both forests, the temporal pattern of R_{WF} paralleled that of R_T (Figure 4.2e). The difference between R_T and R_{WF} was significant throughout the entire period of measurements and reached its maximum in December (23.2%) and its minimum in July (5.1%). In MOF, no significant difference was found during the monitoring period between R_T and R_{WF} .

At annual scale (Table 4.2), the difference in R_T between forest types led to a significantly 10% higher AR_T under MOF (22.1 ± 2.1 Mg C ha⁻¹ year⁻¹) compared to MIF (20.0 ± 2.7 Mg C ha⁻¹ year⁻¹). Based on the conceptual model estimates (see next section), the heterotrophic soil respiration was nearly 30% higher under MOF compared to MIF (8.62 ± 1.56

Table 4.2 – Aboveground annual litterfall, annual fine roots production in forest floor (FF) and in the 0-10 cm mineral soil (MS) layer and annual soil respiration with (AR_T) and without (AR_{WF}) forest floor contribution for the mixed (MIF) and monodominant (MOF) forests (averages $\pm$ standard deviations). Different upper letters in a row indicate significant difference between forests ($p \leq 0.05$). Contributions of the autotrophic (AR_A) and heterotrophic (AR_H) components were estimated using the fitted conceptual model

	MIF	MOF
Aboveground annual litterfall ($Mg\ C\ ha^{-1}y^{-1}$)		
Leaf	2.86 ± 0.49^a	2.79 ± 0.44^a
Fine woody debris	1.75 ± 0.48^a	1.80 ± 0.66^a
Total	4.63 ± 0.80^a	4.57 ± 1.09^a
Annual FR production ($Mg\ C\ ha^{-1}y^{-1}$)		
FF	0.55 ± 0.19^a	0.66 ± 0.31^b
MS	0.32 ± 0.20^a	0.26 ± 0.09^a
Total	0.94 ± 0.22^a	0.89 ± 0.10^a
Annual soil respiration ($Mg\ C\ ha^{-1}y^{-1}$)		
AR_T	20.01 ± 3.01^a	22.10 ± 2.48^b
AR_H	8.62 ± 1.56^a	11.65 ± 2.58^b
AR_A	12.14 ± 2.01^a	12.57 ± 1.20^a
AR_{WF}	15.99 ± 2.14^a	20.99 ± 3.28^b

and $11.65 \pm 2.58\ Mg\ C\ ha^{-1}\ year^{-1}$ in MIF and MOF, respectively; $p < 10^{-7}$) whereas the autotrophic components were similar in both forest types (12.14 ± 2.01 and $12.57 \pm 1.20\ Mg\ C\ ha^{-1}\ year^{-1}$ in MIF and MOF, respectively; $p = 0.18$). On an annual basis, the forest floor contribution to AR_T (paired difference between AR_T and AR_{WF}) was estimated at $3.41\ Mg\ C\ ha^{-1}\ year^{-1}$ (16.1%, $p < 10^{-4}$) and $0.87\ Mg\ C\ ha^{-1}\ year^{-1}$ (3.7%, $p = 0.3$) in MIF and MOF, respectively. Our conceptual model estimated the FF contribution to AR_T at 2.16 ± 0.69 and $2.91 \pm 1.49\ Mg\ C\ ha^{-1}\ year^{-1}$ under MIF and MOF, respectively.

Stepwise regression was carried out to assess the potential drivers of the spatial variation of AR_T . This analysis indicated that 29% ($p < 10^{-5}$) of the spatial variation in AR_T within MIF and MOF could be accounted for by combinations of FRP_{FF} , BA_W , C stocks and pH of the 0-10 cm

Table 4.3 – Parameter estimates ($\pm$ standard error) for a stepwise multiple regression between annual soil C-CO₂ efflux at the plot level and a set of explanatory variables (model $R^2=0.29$ and $p<10^{-5}$) and their relative contributions to the explained variation. The initial model included: (i) leaf litter quantity (annual C inputs as leaf litterfall), (ii) fine root production (FRP) in the FF or in the MS, (iii) stand parameters (forest type, total basal area (BA) and weighed BA (BA_W) and distance to the nearest tree) and (iv) soil parameters (MS and FF C:N ratios, MS and FF C or N stocks, pH of the 0-10 cm MS layer). *, **, *** denote a significant coefficient at $p\leq 0.05$, $p\leq 0.01$ and $p\leq 0.001$

Model terms		Coefficients (sd)	Relative contribution
Intercept		30.99*** (7.06)	na
FR production	FRP _{FF}	3.20* (1.45)	15%
Stand parameters	BA _W	14.05*** (3.91)	37%
Soil parameters	SOC _{MS}	0.11** (0.03)	27%
	pH _{MS}	-3.31 (2.36)	21%

MS layer (Table 4.3). FRP_{FF}, BA_W, C stocks of the 0-10 cm MS layer were positively and significantly related to AR_T whereas pH of the 0-10 cm MS layer exhibited negative relationship with AR_T. AL_L, FRP_{MS}, forest type, BA, distance to the nearest tree, N stocks and C:N ratios of both MS and FF explained no additional variation in AR_T.

4.3.3 R_T and R_{WF} modelling

The conceptual model fitted well to the respiration data for both R_T ($R^2=0.64$) and R_{WF} ($R^2=0.55$). Table 4.4 shows the values of fitted respiration rates (α) and the maximum decomposition rates (k) for R_T and R_{WF}. Considering R_T estimates, FR respiration rates were significantly higher in the FF (5.49×10^{-2} gC g⁻¹ day⁻¹) compared to the 0-10 cm MS layer (0.37×10^{-2} gC g⁻¹ day⁻¹). The k fitted for each layer (O_L, O_F+O_H and 0-10 cm MS layer) was higher under MIF compared to MOF (see Table 4.4). The biggest contrast was shown for O_L which was approxima-

Table 4.4 – Parameter estimates (mean $\pm$ standard error) for the conceptual model of soil respiration (eq. 4.1 to 4.3) fitted to the soil C-CO₂ efflux with (R_T) and without the forest floor (R_{WF}) under MIF and MOF. α (gC-CO₂ g⁻¹ day⁻¹): respiration rates per biomass unit of fine roots in FF and MS; k (day⁻¹): maximum decomposition rates of organic C in O_L, O_F+O_H and MS. *, **, *** denote a significant parameter at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$; na: not applicable

(a) R_T

Parameters		MIF	MOF
R_A	α_{FF}		$(5.49 \pm 0.45^{***}) 10^{-2}$
	α_{MS}		$(0.37 \pm 0.17^*) 10^{-2}$
R_H	k_{OL}	$(2.00 \pm 2.52) 10^{-3}$	$(0.02 \pm 1.99) 10^{-3}$
	k_{OF+OH}	$(4.04 \pm 1.60^*) 10^{-3}$	$(3.17 \pm 1.06^{***}) 10^{-3}$
	k_{MS}	$(2.25 \pm 0.37^{***}) 10^{-3}$	$(1.63 \pm 0.28^{***}) 10^{-3}$

(b) R_{WF}

Parameters		MIF	MOF
R_A	α_{FF}		$(4.19 \pm 0.92^{***}) 10^{-2}$
	α_{MS}		$(0.59 \pm 0.40) 10^{-2}$
R_H	k_{OL}	NA	NA
	k_{OF+OH}	NA	NA
	k_{MS}	$(2.37 \pm 0.67^{**}) 10^{-3}$	$(1.71 \pm 0.33^{***}) 10^{-3}$

tively one hundred times higher under MIF (2.00×10^{-3} day⁻¹) compared to MOF (0.02×10^{-3} day⁻¹).

for both forest types, the maximum decomposition rates and fine root respiration rates were not significantly different between R_{WF} and R_T . Similarly to R_T , FR respiration rates were strongly lower in the MS (0.59×10^{-2} gC g⁻¹ day⁻¹) compared to FF (4.19×10^{-2} gC g⁻¹ day⁻¹) and k of the 0-10 cm MS layer was higher under MIF (2.37×10^{-3} day⁻¹) compared to MOF (1.71×10^{-3} day⁻¹).

Based on the sensitivity analysis, the difference in the size of SOC stocks (FF plus 0-10 cm layer) between forest types was shown to be the greatest contributor (169.3 and 189.2 % for AR_T and AR_H , respectively)

Table 4.5 – Contribution of selected drivers of soil respiration involved in the conceptual model (parameters: α and k ; environmental variables: SVWC, T , FR biomass, SOC stocks) to the difference in annual autotrophic and heterotrophic soil respiration between forest types. Negative values indicate that the difference in respiration related to the considered driver is opposite to the observed difference; na: not applicable

		AR _A	AR _H	AR _T
Coefficients contribution		na	-114.8 %	-99.6 %
Variables contribution	Pedoclimatic (SVWC, T)	203.61 %	23.8 %	44.9 %
	FR biomass	-102.1 %	na	-13.4 %
	SOC (FF, MS)	na	189.2 %	169.3 %

in explaining the higher AR_T and AR_H under MOF compared to MIF (Table 4.5). Although enhanced by the significantly higher SVWC and soil temperature under MOF (44.9 and 23.8 % for AR_T and AR_H, respectively) these differences are strongly limited by the lower k values estimated for MOF in O_L, O_F+O_H and MS layers (-99.6 and -114.8 % for AR_T and AR_H, respectively). The slight difference in AR_A between MIF and MOF (less than 4 %) was strongly favoured by the most suitable pedoclimatic conditions under MOF (203.6 %) but counterbalanced by the slightly higher fine roots biomass reported for MIF (-102.1 %).

4.4 Discussion

4.4.1 Annual soil C-CO₂ fluxes and their components

R_T

Annual R_T (AR_T) observed in MIF (20.0±3.0 Mg C ha⁻¹ year⁻¹) are significantly 10% lower compared to MOF (22.1±2.5 Mg C ha⁻¹ year⁻¹) in agreement with the difference in mean daily R_T reported between forest types. Furthermore, these results are similar to those estimated by previous studies in old-growth tropical forests: from 16.2 to 24.4 Mg C ha⁻¹ year⁻¹ [Davidson et al., 2000; Sotta et al., 2004; Epron et al., 2006]. According to Litton et al. [2007], between 30 and 60%, even

more, of the C assimilated by photosynthesis in forested ecosystems is allocated to roots, this amount is referred to as total belowground C allocation (TBCA). For soils that are near steady state with respect to total organic C storage, [Raich and Nadelhoffer, 1989] showed that TBCA can be estimated at annual scale as soil-surface CO₂ efflux (AR_T) minus aboveground fine litterfall (AL_L+AL_W). On this basis, slightly higher TBCA values ($p < 10^{-2}$) were observed for MOF (17.23 ± 2.56 Mg C ha⁻¹ year⁻¹) than for MIF (15.37 ± 2.98 Mg C ha⁻¹ year⁻¹). The TBCA values are higher than those observed for temperate and boreal forests [Davidson et al., 2002] and consistent with the range of 13.40 to 15.20 Mg C ha⁻¹ year⁻¹ reported for tropical primary forest in the Amazon [Davidson et al., 2002; Litton et al., 2007]. Strongly correlated with net primary productivity [Raich and Nadelhoffer, 1989; Nadelhoffer et al., 1998], these high TBCA highlight the key role these forest types can play in global C cycle in the current climate change context. Based on the regression between AR_T and total annual litterfall (AL_L + AL_W) for worldwide forest ecosystems proposed by Davidson et al. [2002], AR_T measured in the present study were consistent with expected (18.3 Mg C ha⁻¹ year⁻¹) values estimated from our local mean total annual litterfall (4.60 Mg C ha⁻¹ year⁻¹, Table 4.2).

FF contribution to R_T

By subtracting CO₂ efflux measured in the chambers with litter removal from the respiration measured in the control chamber ($R_T - R_{WF}$), we were able to estimate the FF contribution to R_T. At annual scale, FF respiration reached 3.41 ± 3.28 (16.1%, $p < 10^{-4}$) and 0.87 ± 2.88 (3.7%, $p = 0.3$) Mg C ha⁻¹ year⁻¹ in MIF and MOF, respectively. In MIF, the reduction in the soil respiration due to litter exclusion was similar to the value measured by Sayer et al. [2007] (20% in average, from 7 to 38%) and Leff et al. [2012] (22%) in old-growth moist lowland tropical forest.

Based on the conceptual model, the FF contribution to AR_T was estimated to 2.16 ± 0.69 and 2.91 ± 1.49 Mg C ha⁻¹ year⁻¹ in MIF and MOF, respectively resulting in similar relative contribution (10.2 and 12.4 % in MIF and MOF, respectively). While both estimates of FF contribu-

tion were comparable for MIF, the FF contribution estimated from our conceptual model for MOF (12.4 %) was strongly higher compared to estimates from our litter removal experiment (3.7 %).

In forested ecosystems, the FF acts as a natural barrier by increasing resistance of CO₂ diffusion from soil to the atmosphere. Litter removal may induce some artefacts by increasing soil CO₂ efflux leading to an overestimation of R_{WF} and thus to an underestimation of the FF contribution to R_T [Luo and Zhou, 2006]. The stronger FF accumulation under MOF compared to MIF may therefore lead to a strong underestimation of the FF contribution.

Contributions of R_A vs R_H to R_T

Our conceptual model allowed to separate soil respiration between the autotrophic and heterotrophic components, both related to contrasted processes. The balance between the R_A and R_H components slightly differed between MIF and MOF. R_A and R_H contributed equally (approximately 50% each) to R_T under MOF (12.57 ± 1.20 and 11.65 ± 2.58 Mg C ha⁻¹ year⁻¹, respectively for R_A and R_H , Table 4.2) whereas R_H accounted only for 41% (8.62 ± 1.56 Mg C ha⁻¹ year⁻¹) of AR_T under MIF. Absolute and relative AR_H and AR_A are comparable to those previously reported for tropical forests [Malhi et al., 2011; Hashimoto et al., 2015; Tian et al., 2015].

4.4.2 Seasonal pattern in soil respiration

In both forest types, R_T exhibited a strong relationship with SVWC (Figure 4.3a) explaining more than 50% the observed variation in respiration. Therefore, the strong seasonality observed in R_T is strongly related to the seasonality of SVWC; the highest rates of soil respiration were reported during rainy seasons (Figure 4.2a and e). Through litter removal experiment, our results showed that FF contributed at daily scale in average to 12.27 % ($p < 10^{-5}$) in MIF but not significantly under MOF. In MIF, FF contribution was characterised by a strong seasonality

with a maximum reached in December (23.10 %) and a minimum in July (5.45 %).

These observations emphasized the well-known relationships between R_T and SVWC [Orchard and Cook, 1983]. In both MIF and MOF, the square root curve used to model R_T in function of SVWC (Figure 4.3a, $R_T = -5.27 + 18.99 \times \sqrt{SVWC}$, $R^2=0.54$) highlighted the decreasing influence of SVWC with increasing soil moisture. Whereas soil moisture exceeding field capacity has been shown to reduce R_T in tropical forest [Schwendenmann et al., 2003; Sotta et al., 2006; Wood et al., 2013], no suppressing effect was reported in this study. However, SVWC exceed $0.5 \text{ m}^3 \text{ m}^{-3}$ in only 8% of cases in MIF and MOF making it difficult to observe the inversion of the relationship between R_T and SVWC.

In average, soil moisture was significantly 13% higher in MOF compared to MIF. Despite similar rainfall in both forest types, greatest differences in SVWC were observed during the main rain season (September-December) (Figure 4.2a). In addition, we observed a delayed reaction (increase *vs.* decrease) of SVWC to precipitations. Acting as an important insulator, the higher FF C stocks under MOF may slow the potential rate of drying in the mineral soil [Keith et al., 2010]. Moreover, through its influence on soil aggregation and associated pores distribution [Rawls et al., 2003], SOC stocks has been shown to enhance soil water holding capacity.

Through its implication in microbial and root activity as well gas diffusion, soil temperature is often identified as the dominant factor in controlling temporal variation of soil CO_2 efflux in boreal and temperate ecosystems [Lloyd and Taylor, 1994; Vargas et al., 2010]. In MIF and MOF, where soil temperatures are high and relatively constant (Figure 4.2b), the absence of relationship between R_T and soil temperature is not surprising (Figure 4.3b) as previously reported by Davidson et al. [2000].

In addition to soil climatic variables, seasonal trend in R_T and its components are strongly influenced by net primary productivity through above- and belowground litter production. Due to the addition of easily-

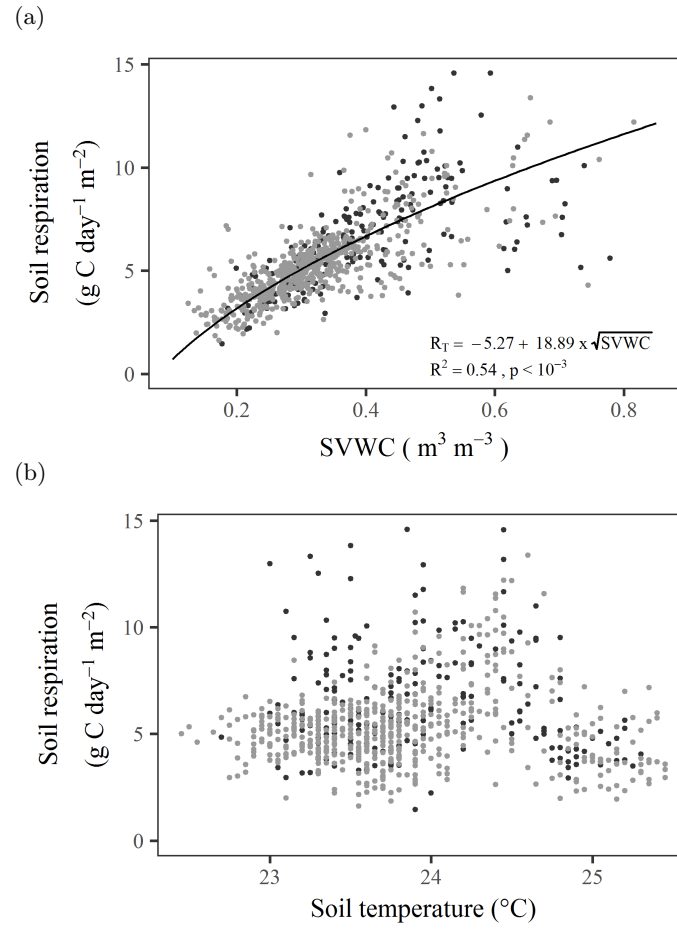


Figure 4.3 – Relationships between total soil respiration and soil volumetric water content (SVWC) (a) or soil temperature (b) in the mixed (MIF, in grey) and monodominant (MOF, in black) forests

decomposable organic substances to the soil, increased litter inputs may accelerate decomposition mainly by stimulating decomposers activity [Kuzyakov, 2002; Leff et al., 2012]. Increases in R_T and FF contribution to R_T reported in November and December after peak in litterfall and FR biomass may reflect this priming effect (Figure 4.2). However, net primary productivity is largely determined by rainfall and temperature, which makes it difficult to separate the individual contribution of each factor.

4.4.3 Spatial variability of soil respiration

In addition to high temporal variability, great spatial variation in R_T was also observed in both forest types with AR_T values ranging from 14.36 to 28.03 Mg C ha⁻¹ yr⁻¹ and from 17.49 to 28.68 Mg C ha⁻¹ year⁻¹ in MIF and MOF, respectively. Stepwise regression revealed that BA_W , C stocks in 0-10cm, pH of the 0-10 cm MS layer and FRP_{FF} were the factors most strongly related to AR_T whereas AL_L , FRP_{MS} , forest type, BA, distance to the nearest tree, N stocks and C:N ratios of both MS and FF explained no additional variation in AR_T . The most critical variable explaining the spatial variation of AR_T was BA_W (Table 4.3). This result suggests that soil respiration is the result of a large set of biological processes related to the surrounding trees [Luo and Zhou, 2006; Katayama et al., 2009]. Trees are involved, either directly (root respiration) or indirectly (root derived rhizosphere respiration, production of carbon substrates for microbial respiration), in most of these processes. In addition, through changes in microclimatic conditions such as air temperature, air relative humidity and solar radiation, higher tree density or BA can enhance soil respiration. As expected, BA_W suggest a weaker effect more distant is the surrounding tree. Similarly to our processes-based conceptual model, the stepwise regression highlighted the major role of the SOC stocks in explaining the variation in R_T . Through increase in availability of C substrates for microorganisms, SOC_{MS} significantly enhanced AR_T [Raich and Tufekciogul, 2000]. Strongly higher under MOF, SOC_{MS}

influence on AR_T largely reflects the forest effect which are, thus, not selected by the stepwise regression.

As major source of belowground C inputs, FR production and turnover is associated to soil respiration [Finér et al., 2011]. Contrary to FRP_{MS} , FRP_{FF} was strongly linked to AR_T spatial variation. This result is consistent with the higher FRP in FF compared to MS reported in both forest types. Surprisingly, negative relationship was found between pH of the 0-10 MS soil layer and AR_T . Usually, increase in pH have a positive effect on the growth and proliferation of microbes and thus on heterotrophic soil respiration. Negative effect of pH on soil respiration may be the result of the strong negative relationship between soil pH and MS C stocks in both forest types also reported by Cassart et al. [2016] in MIF and MOF. Whereas litter input is generally strongly related with soil respiration, AL_L explained no additional variation in AR_T under both forest types. However, in MIF and MOF, the variability of litterfall production was considerably lower compared to other explanatory variables. Indeed, the mean coefficient of variation of AL_L for both forests was approximatively 18% against 38, 73 and 84% for MS C stocks, BA_W and FRP_{FF} , respectively.

4.4.4 Parametrization of the conceptual model

Although the difference was slight, our conceptual model ($R^2=0.64$) explained a higher proportion of the variance in R_T compared to linear semi-empirical model considering only soil climate parameters; SVWC and T ($R^2=0.54$, see Appendix 18 for model parameters). In addition, an excellent agreement was found between the set of parameters estimated for R_T and R_{WF} .

Higher respiration rates of fine root (α) in the litter layer compared to the MS are consistent with their higher annual productivity suggesting higher activity (Table 4.2). Indeed, although litter layer exhibited a FR biomass two times lower compared to MS in both MIF and MOF, FR production in FF was approximatively 50% higher. The hypothesis

of a higher FR activity in FF compared to MS is also supported by the selection of FRP_{FF} , not FRP_{MS} , in the stepwise procedure used to explain the spatial variation of AR_T (Table 4.3). Previous studies of superficial root mat in Amazonian forest have showing higher root proliferation in the litter layer [John, 1983; Cuevas and Medina, 1988].

The maximum decomposition rates (k) fitted by our conceptual model (Table 4.4) for the FF ranged from 0.02×10^{-3} to $4.04 \times 10^{-3} \text{ day}^{-1}$. Those estimates are consistent with the mean k of 6.10×10^{-3} (from 0.80×10^{-3} to $12.00 \times 10^{-3} \text{ day}^{-1}$) reported for litter layer in tropical forest [Hättenschwiler et al., 2011]; they are also in agreement with decay rates obtained from the ratio of annual litter production ($AL_L + AL_W$) to steady-state accumulation of forest floor (FF C stocks) (Olson, 1963) which amounted to 5.34×10^{-3} and $2.12 \times 10^{-3} \text{ day}^{-1}$ in MIF and MOF, respectively.

Regarding the MS layer, the k values related to the conceptual model (Table 4.4) were comparable to the initial values of decay rates from the incubation experiment (k_{inc}) for MIF ($2.70 \pm 0.74 \times 10^{-3} \text{ day}^{-1}$) and MOF ($1.82 \pm 0.62 \times 10^{-3} \text{ day}^{-1}$) (see Appendix 19). Although k_{inc} strongly decreased with time, the difference of k_{inc} between forest types (in average $31.2 \pm 1.4\%$) remained constant during the experiment and are consistent with the difference of k between forest types reported for the conceptual model (17.8%).

Though the differences were not significant, the lower k values for the O_L , $O_F + O_H$ and MS layers in MOF compared to MIF are consistent with the greatest C accumulation in soil (FF + MS topsoil) under MOF reported in this study for otherwise comparable aboveground (4.63 and $4.57 \text{ Mg C ha}^{-1} \text{ y}^{-1}$) and belowground C inputs (0.94 and $0.89 \text{ Mg C ha}^{-1} \text{ y}^{-1}$), and to the limited organic matter decomposition under *G. deweyrei* previously reported by Torti et al. [2001] and Peh et al. [2012].

4.4.5 What are the drivers of soil respiration differences between MIF and MOF?

By applying the conceptual model to a "mean plot" in which we allowed each explanatory variable to vary according to forest type through our sensitivity analysis, we were able to estimate the relative contribution of the model coefficients and variables to the difference in AR_A and AR_H between MIF and MOF (Table 4.5). Whereas the difference in AR_A between forest types was not significant (3.2%), AR_H was approximately 30% higher under MOF compared to MIF (Table 4.2). Pedoclimatic variables (SVWC and T) and SOC stocks were the main contributors to the difference in soil CO_2 efflux between forest types, by their effects on R_A and R_H respectively (Table 4.5).

AR_A

According to our results, the most favourable pedoclimatic conditions (SVWC and T) under MOF explained the slightly higher AR_A under MOF (12.57 Mg C ha⁻¹ y⁻¹) compared to MIF (12.14 Mg C ha⁻¹ y⁻¹). In tropical forests, changes in soil temperature and moisture often result from light availability variations. Soil moisture enhance root activity and root growth resulting in higher specific root respiration [Luo and Zhou, 2006]. Nevertheless, the slightly higher FR biomass in MIF (2.75 Mg ha⁻¹) compared to MOF (2.59 Mg ha⁻¹) tends to reduce the difference in AR_A (-102.1 %).

The amount of CO_2 produced through root respiration is determined by the root biomass and specific root respiration (α), regulated by soil temperature and moisture. α may also be influenced by root morphology (e.g. tissue density, diameter and specific root length), age and N concentration [Makita et al., 2012]. Nevertheless, scaling the direction and magnitude of the relationships between α and all this biotic influencing factors is problematic because of a lack of experimental data under tropical rainforests [Luo and Zhou, 2006; Hopkins et al., 2013]. Therefore, our conceptual model only considered the most important factors (FR biomass, T and SVWC) reported for these ecosystem.

AR_H

The difference in AR_H was mostly related to the much stronger C accumulation observed under MOF (Table 4.5). SOC storage (MS topsoil + FF) was almost two times higher in MOF (28.83 ± 6.22 Mg C ha⁻¹) compared to MIF (16.22 ± 2.81 Mg C ha⁻¹). The greatest C accumulation under MOF in the Yoko Reserve is consistent with the C stocks reported by Cassart et al. [2016]. This difference in SOC accumulation results from a limitation of the decomposition rate under MOF through a set of litter traits exhibited by *G. dewevrei* related to organic matter recalcitrance [Peh et al., 2012; Kearsley et al., 2017] which is consistent with the parameters fitted with our conceptual model. The difference in estimated maximum decomposition rates between forest types were not significant but contributed to buffer the contrast in AR_H; the higher *k* under MIF reduced the difference in AR_H (-114.8%, Table 4.5). Unlike AR_A, the difference in SVWC and soil temperature only marginally affected AR_H by accentuating the difference in soil C-CO₂ efflux between forests by only 23.8%.

4.5 Conclusions

Despite a difference of soil respiration between forest types that did not exceed 10%, C allocations to heterotrophic soil respiration was *ca.* 30% higher under MOF compared to MIF. Our results indicate that spatial and temporal variation of soil respiration and its components are controlled by different drivers. Whereas seasonal trends are driven by pedo-climatic variables such as soil moisture and soil temperature, the spatial variation and difference between forest types in heterotrophic soil CO₂ efflux are mostly related to biotic factors and more particularly to the functional traits related to recalcitrance exhibited by *G. dewevrei*, in MOF. Low root and leaf N concentrations leads to the predominance of heterotrophic component under MOF through the strong C accumulation in topsoil (mineral soil and forest floor).

As MIF and MOF co-exist on a large range of soils [Hart et al., 1989], it remains to determine whether the control of this biotic and abiotic factors on seasonal and spatial variations of soil respiration and its components would be similar in different ecological conditions.

Chapter 5

General discussion

The major aim of this thesis was to better understand the influence of the forest type and species composition on soil C dynamics in tropical oldgrowth forests. In the tropics, highly diverse forests are often found to be adjacent to forests where more than 60% of the canopy-level trees belong to one single species, called monodominant forests. In the Congo basin more specifically, *G. dewevrei* is the main species found to be naturally dominant on large patches [Hart et al., 1989].

Whereas several studies dealt with the impacts of *G. dewevrei* dominance on selected ecosystem functions, this thesis is the first research project that consistently compares the main above- and belowground C stocks and fluxes between *G. dewevrei* monodominant forest and adjacent *S. zenkeri* mixed forest in similar ecological conditions. Detailed investigation of the impacts of species composition on C cycle in tropical forests is of major importance in order to better assess the potential role of tropical forests in climate mitigation through improved global C dynamics models.

In this section, we provide a general overview and an integrated discussion of the key findings of this thesis. Thereafter, we suggest directions for further research. The main results discussed in the present section are summarized in Figure 5.1.

5.1 Key findings

The two forest types were located in the Yoko forest reserve (Kisangani, DRC) next to each other, in similar climatic, topographic and edaphic conditions. The soils under both forests were nutrient poor, deeply weathered and acidic ($\text{pH} < 4.8$) Xanthic Ferralsols. Both MIF and MOF exhibited topsoil (0-10 cm MS layer) with sand content higher than 86% (Table 2.1, chapter 2). This sandy texture decreased slightly with depth while the clay content increased in MIF and MOF.

However, species composition and diversity strongly differed between the two forest types. The *G. dewevrei* monodominant forest exhibited signif-

icantly lower species richness compared to the adjacent mixed forest as quantified by the Shannon Diversity Index (1.49 and 3.12 in MOF and MIF, respectively). In addition, while *S. zenkeri* accounted for 28.2% of the total BA in MIF, the contribution of *G. dewevrei* to total BA accounted for 73.1% in MOF allowing this forest to be defined as monodominant.

Similar ecological conditions is an important prerequisite to assess the influence of forest types on C sequestration. Without a careful control over environmental conditions and other potentially confounding factors, direct comparison of ecosystem functions between forest types probably often results in biases because of inherent difference in site fertility [Augusto et al., 2015].

As shown in Figure 5.1, great differences were reported in forest floor C stocks between MIF and MOF in the Yoko reserve. A threefold C accumulation in FF was shown in forests dominated by *G. dewevrei*, in agreement with previous studies comparing MOF to adjacent mixed forests in Central Africa [Torti et al., 2001; Peh et al., 2012]. Similarly, C stocks in mineral soil (down to 220 cm depth) were approximatively 45% higher in MOF compared to MIF and this difference was particularly strong for topsoil (0-25 cm). Contrary to previous studies from temperate and boreal forests where tree species impacts were found to be limited to the topsoil [Augusto et al., 2003; Vesterdal et al., 2013], MOF consistently showed a significantly greater C accumulation in the FF and MS down to 100 cm depth.

In given climate and soil conditions, SOC pools are determined by the balance between C inputs through primary productivity (above- and belowground litter production) and outputs through the decomposition process.

Although initial decay rate of OM is strongly determined by OM quality and molecular properties, von Lützow et al. [2006] have shown that OM long term persistence in soil is mainly influenced by spatial inaccessibility of OM for decomposer organisms (occlusion, intercalation, hydrophobicity and encapsulation) and by stabilization through interaction with

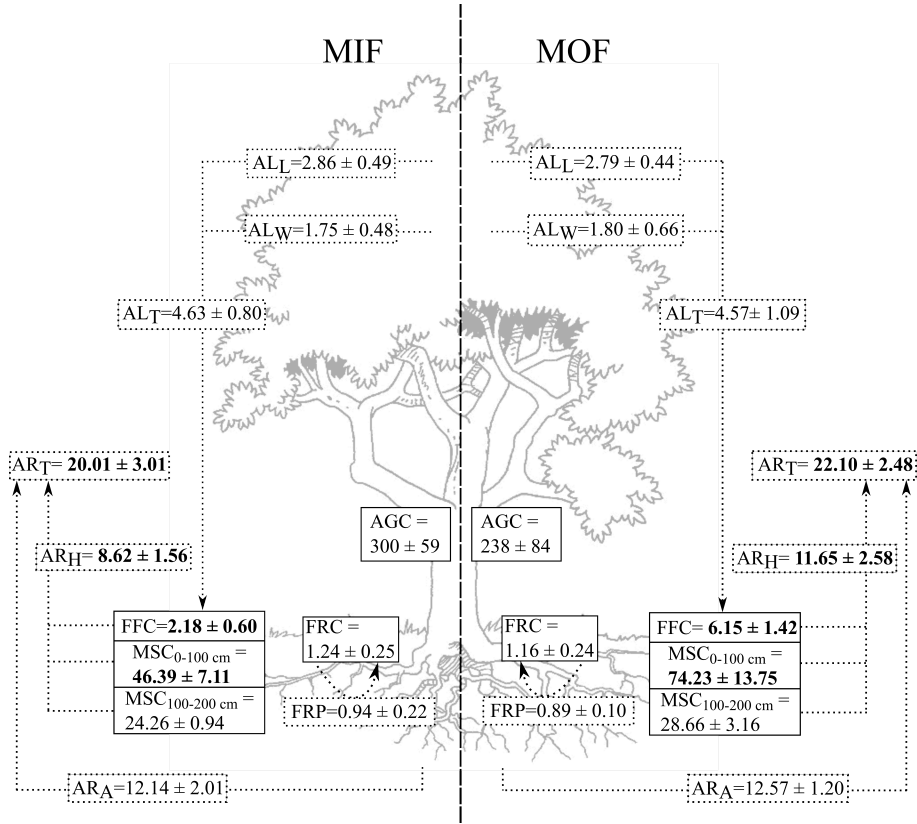


Figure 5.1 – Main C stocks and fluxes estimated in MIF and MOF, in the Yoko Reserve. AGC, aboveground biomass C stocks; AL_L , annual leaf litterfall; AL_W , annual fine woody debris litterfall; AL_T , annual fine litterfall ($AL_F + AL_W$); AR_A , annual soil autotrophic respiration; AR_H , annual soil heterotrophic respiration; AR_T , annual total soil respiration ($AR_A + AR_H$); FRC, fine roots C stocks in FF and 0-10 MS layer; FRP, fine roots production in FF and 0-10 MS layer; FFC, forest floor C stock ($O_L + O_F + O_H$); $MSC_{0-100\text{ cm}}$, 0-100 cm mineral soil layer C stocks; $MSC_{100-200\text{ cm}}$, 100-200 cm mineral soil layer C stocks. All units are Mg C ha^{-1} year $^{-1}$ and Mg C ha^{-1} for C fluxes and stocks, respectively. C fluxes and stocks highlighted in bold differ significantly ($p < 0.05$) between forest types.

mineral surfaces and metal ions. In the present case, however, geochemistry could not explain the large difference in C accumulation between forests. Although significant for some mineral horizons, the difference

in clay content between forests remained quite limited ($<5\%$; Table 2.1, chapter 2); in addition, the higher C concentrations were associated with lower clay content under MOF which is contrary to expectations.

OM inputs through above- and belowground litter production were strictly similar in both forest types (Figure 1). Over one year, 4.63 and $4.57 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ fell on the ground under MIF and MOF, respectively. Furthermore, annual fine roots production in the FF and in the 0-10 cm MS layer were not significantly different between forest types during our measurement period (0.94 and $0.89 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ in MIF and MOF, respectively). As a result, the contrasting SOC stocks in MS and FF could not be explained by difference in OM input between MIF and MOF; rather, they should be related to contrasted C emission through the decomposition of the fresh litter, forest floor and OM in the MS.

In our field incubation experiment, the fresh litter of the eight dominant tree species have shown contrasted initial decomposition rates. The greatest difference in initial decay rates was reported between *S. zenkeri* and *G. dewevrei*, the most abundant species under MIF and MOF, respectively. Three times lower litter mass loss of *G. dewevrei* compared to a mixed-litter typical of *S. zenkeri* forests has already been observed by Torti et al. [2001] and Peh et al. [2012]. An important proportion of the three-fold variation in initial decay rate across species was explained by the chemical quality of the litter through its position along the leaf economics spectrum (LES) (Figure 3.3, chapter 3).

Aboveground leaf litterfall collected under MIF and MOF exhibited contrasted functional traits. High Ca, K, Mg, Mn, N, P and S concentrations were observed in MIF whereas higher Si concentrations as well as CN, CP, CS and NP ratios were found in MOF, resulting in contrasted positions along the LES (Figure 2.1 and Table 2.2, chapter 2). The position of the litterfall under MIF and MOF along the LES was mainly related to the chemical quality of the leaf litter of their respective dominant species (*S. zenkeri* vs. *G. dewevrei*). Those contrasted positions suggest different life-history strategies [Wright et al., 2004; Reich, 2014]. On one side, related to low nutrients concentrations, MOF was associated

with 'conservative strategies', which is typical of evergreen species such as *G. dewevrei*; the other side of the LES was dominated by deciduous tree species abundant under MIF, including *S. zenkeri*, characterised by 'acquisitive strategies' [Givnish, 2002].

In chapter 4, we developed a process-based conceptual model parameterized by environmental variables (pedoclimatic variables, SOC stocks and FR characteristics) measured in MIF and MOF, which allowed us to estimate a decomposition rate for each considered soil layer; O_L , O_F+O_H and 0-10 cm MS layer (Table 4.4, chapter 4). In agreement with the results from our field decomposition experiment, the non-decomposed fallen plant material (O_L) exhibited strongly higher k under MIF ($2.00 \times 10^{-3} \text{ day}^{-1}$) compared to MOF ($0.02 \times 10^{-3} \text{ day}^{-1}$). For MOF, the decay rate related to the O_F+O_H layer further increased compared to the O_L suggesting an increase in k with OM breakdown; this was consistent with the results of chapter 3, where k_{app} of *G. dewevrei* litter was found to increase with time in the early phase of decomposition (up to 4 months of incubation). Lower initial decomposition rate are not uncommon and can be related to a delayed colonization by decomposers due to recalcitrant compounds in tissues (e.g. lignin) [Freschet et al., 2012b; Cornwell and Weedon, 2014].

Our conceptual model allowed us to show slightly different contributions of R_A and R_H between MIF and MOF (Figure 5.1). Autotrophic and heterotrophic components contributed about equally to R_T in MOF while R_A dominated total soil CO_2 in MIF (Table 4.2, chapter 4). Through the twofold SOC accumulation, heterotrophic contribution to R_T was approximatively 30% higher under MOF compared to MIF (Table 4.5, chapter 4).

Through a set of above- and belowground traits related to recalcitrance, the dominance of *G. dewevrei* has been shown to strongly influence the forest functioning, especially SOC sequestration. By decreasing the decay rate of fresh organic matter and of soil organic matter, the low-quality litter of *G. dewevrei*, together with some other traits, increased C accumulation in soil under MOF compared to MIF leading to differ-

ent soil CO₂ efflux partitioning. However, the dominance of *G. dewevrei* did not appear to limit the aboveground C storage nor the net primary productivity (as inferred from similar above- and belowground litter production).

5.2 Methodological issues

5.2.1 Pseudo-replication

Before installing the plots, we performed an intensive field survey in the Yoko reserve to find out replicated blocks containing patches of both forest types in similar site conditions. However, we were unable to identify such conditions locally. As it was not feasible too investigate other forests within this PhD, we need to acknowledge the power of our statistical design is weakened by repeating plots within a limited number of forest patches of each type, rather than using many forests.

5.2.2 Unbalanced number of plots

Based on the well known much lower species diversity reported for the *G. dewevrei* monodominant forests compared to their adjacent mixed forests in Central Africa, we expected lower variability in C stocks and C fluxes under MOF. In addition, we could only find relatively small areas of MOF with site conditions similar to those associated with MIF. For those two reasons, we set up approximatively the double of plots under MIF compared to MOF.

5.2.3 Soil respiration

Based on our conceptual model estimates (chapter 4), the contribution of litter decomposition to total soil CO₂ efflux derived from the forest floor removal appeared to be strongly underestimated under MOF through a substantial stronger accumulation of organic matter on the ground. Our

method consisted of removing the forest floor only during the measurement day while keeping it during the rest of the period. As previously explained, this caused a reduction of the resistance to CO_2 through a chimney effect which was further reinforced by the forest floor thickness. However, keeping the forest floor on the ground between each measurement period allowed us to avoid the bias from the priming effect. Indeed, the decomposition of the underlying organic matter could be accelerated or delayed by fresh labile inputs, with corresponding impacts on the RH flux..

5.3 Suggestions for further research

5.3.1 Expansion of the study case to different ecological conditions

G. dewevrei strongly affected SOC dynamics in the highly weathered, acidic and sandy soils of the Yoko reserve. Nevertheless, our study case cannot be assumed to be representative of the entire Congo basin. Pair-wise patches of *G. dewevrei* monodominant forests and highly diverse forests co-exist on a large range of ecological conditions over the zone, such as in Cameroon where *G. dewevrei* monodominant forests occur on clayey soils. Therefore, it remains to determine if the differences observed on those highly weathered sandy soils would be similar in other ecological contexts or whether difference in SOC accumulation would rather interact with site conditions.

5.3.2 Roots contribution to C storage and autotrophic soil respiration

Most estimates of tropical forest biomass overlook belowground biomass (coarse and fine roots), mainly because of methodological issues related to measurement. Roots biomass is most often estimated as a fraction of the aboveground biomass through the root:shoot ratio. In average,

Cairns et al. [1997] and Mokany et al. [2006] reported a root:shoot ratio value of 0.24 in tropical moist forests. However, root:shoot ratio values can vary substantially leading to highly uncertain roots contribution to C storage. A better understanding of the influence of species composition, soil properties and climate on root:shoot variability is needed to improve the accuracy of the few allometric models used for belowground biomass.

In chapter 4, our concept-based model only considered fine roots in the forest floor and in the 0-10 cm mineral soil. Deeper fine roots also contribute to the autotrophic component of soil respiration and could help to enhance our understanding of the temporal and spatial variations of the soil respiration reported in this study.

5.3.3 Decomposition in multiple species mixture and belowground decomposition

In chapter 3, we compared the decomposition rates of all pure and two-species litters related to a pool of eight abundant tree species from MIF and MOF with contrasting litter chemistries. On average, litter-mixture effects on decomposition were quite limited with a maximum of 3.21% shift in mass loss on average after 1 month. Depending on the associated tree species, this weak non additive effect could arise either from opposite trends for each member of the pair, or for a complete lack of interactions. As the most species-rich plant communities, tropical forests rarely exhibit such pairwise species combination in litter layers under natural conditions. Therefore, further investigations are needed to determine if such interactions are found in litter mixture including a greater number of species in tropical forests.

Furthermore, we only focused on the decomposition of the leaf litter which is relatively easily accessible, and did not consider other major plant parts such as root litter. Yet *G. dewevrei* can be expected to substantially influence the decomposition processes of other plant tissues through its conservative strategy. Therefore, to improve our understanding of SOC accumulation under MOF, a proper assessment of

roots decomposition processes under tropical forests would certainly be needed.

5.3.4 Functional traits and belowground C cycle in tropical forests

This thesis highlights the need to improve our mechanistic knowledge of the spatial variation in belowground C dynamics to further determine the influence of forest type and species composition on soil C sequestration. Through our three research chapters, we pointed out the major impacts of some root and leaf traits on SOC accumulation, leaf litter decomposition and soil respiration in oldgrowth tropical forests. In this context, it is crucial to identify easily measurable, cost-effective above- and below-ground traits. However, interspecific and intraspecific variations in functional traits remain poorly studied. More specifically, global plant trait databases lack substantial data from the Congo Basin. Our results highlight that reliable assessment of the global whole plant economics spectrum should prove valuable in modelling SOC dynamics in tropical forests.

5.3.5 Deep SOC accumulation under *G. dewevrei* monodominant forest

Contrary to numerous reports from temperate and boreal forests where tree species impacts are limited to the topsoil, greater C accumulation was also reported in the MS down to 100 cm depth under the *G. dewevrei* monodominant forest compared to its adjacent mixed forest in the Yoko reserve. Because deep soil C typically has C^{14} dates in the hundreds and/or thousands of years [Trumbore, 2000], deeper SOC accumulation can be related to ancient vegetation covers with a distinctly species composition than today. While we have not detected any charcoal presence in this thesis, pedoanthracological studies under MIF and MOF could be useful to gain a better understanding of past forest dynamics.

5.4 Implications for forest C mitigation initiatives

Translating the vision of the National REDD+ Strategy into concrete actions in the Republic Democratic of Congo, the DRC REDD+ Investment Plan was adopted in 2013. However, the implementation of the REDD+ mechanism needs to be supported by accurate baseline of C storage and emissions at the national level. Through a better understanding of the drivers behind the variability of the SOC dynamics, several aspects of this thesis may prove useful for policymakers. Tropical rainforests in the Congo basin comprise a large range of tree species diversity from ecosystems where nearly one single tree species dominates in the upper canopy layer, such as MOF, to highly diverse forests. In addition to emphasize the major contribution of soil to C sequestration in tropical rainforests, our results show that contrasted community functional trait compositions may lead to contrasted SOC dynamics and more specifically to contrasted SOC accumulations in tropical rainforests. Therefore, our study highlights that a reliable assessment of the global whole tree species economics spectrum can provide valuable information to support current and future mitigation initiatives such as forest plantation and improved forest conservation.

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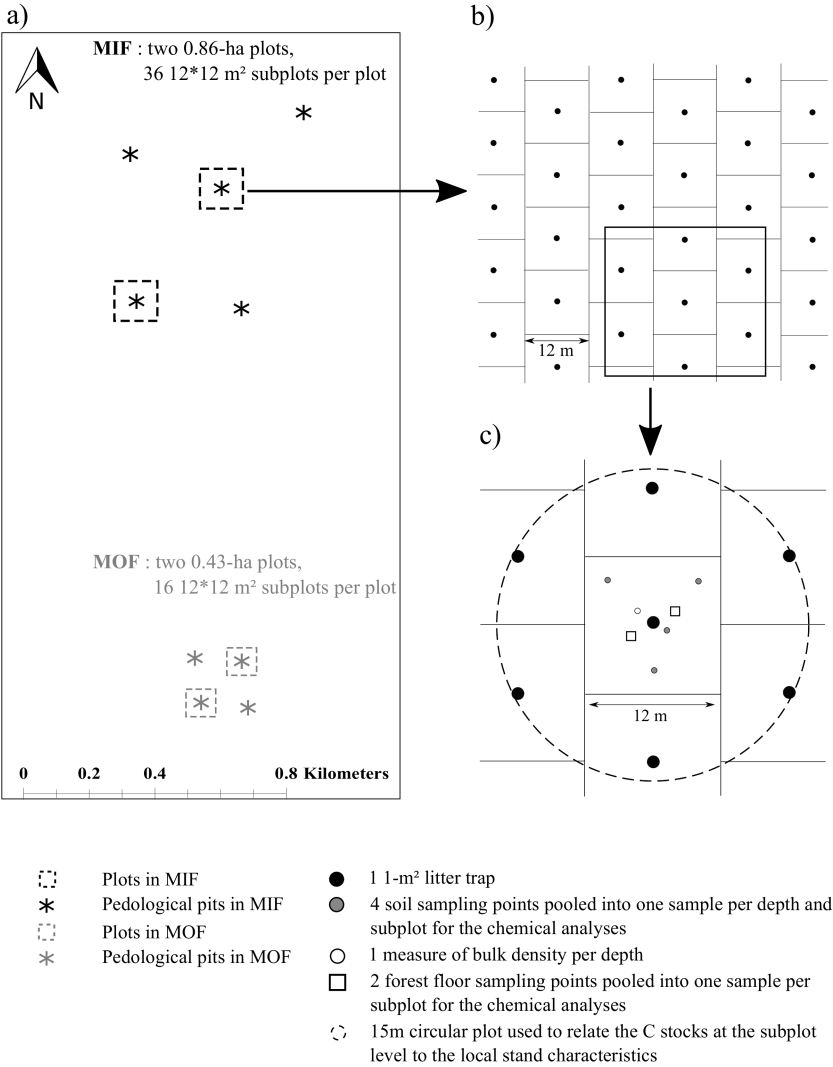
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Appendices



Appendix 1 – Sampling plan and sampled locations in MIF and MOF. a) Study area, indicating the location of the plots and pits in MIF and MOF. b) Systematic grid-based design within each plot. c) Sampling of litterfall, forest floor, mineral soil, and soil bulk density at the subplot level; the dashed circle indicates the 15-m radius circular plot used to relate the C stocks at the subplot level to the local stand characteristics.

Appendix 2 – List of sampled tree species. Family, scientific name, observed DBH range, number of trees sampled for height allometry and number of trees sampled for wood specific gravity (WSG).

Sp	MIF		MOF	
	% BA	% N	% BA	% N
<i>Afrostryax lepidophyllus</i> Mildbr.	0.24	0.76	0.03	0.87
<i>Afzelia bipindensis</i> Harms	0.1	0.15		
<i>Aidia micrantha</i> (K.Schum.) F. White	0.59	4.28	0.17	1.27
<i>Albizia gummifera</i> (J.F.Gmel.) C.A.Sm.	1.04	0.31		
<i>Allanblackia floribunda</i> Oliv.			0.03	0.58
<i>Alstonia boonei</i> De Wild.	3.88	0.46		
<i>Anonidium mannii</i> (Oliv.) Engl. & Diels	2.99	3.67	1.02	3.86
<i>Anthonothea fragrans</i> (Baker f.) Exell & Hillc.	1.34	0.31	0.53	0.59
<i>Anthonothea macrophylla</i> P.Beauv.	0.02	0.15	0.03	0.29
<i>Anthonothea pynaertii</i> (De Wild.) Exell & Hillc.	0.09	0.31		
<i>Antiaris toxicaria</i> Lesch.	0.03	0.15		
<i>Antrocaryon nannanii</i> De Wild.	0.54	0.15		
<i>Autranella congolensis</i> (De Wild.) A.Chev.			0.02	0.29
<i>Blighia welwitschii</i> (Hiern) Radlk.			0.02	0.29
<i>Carapa procera</i> DC.	0.05	0.31	0.76	3.18
<i>Celtis mildbraedii</i> Engl.	2.31	2.45		
<i>Celtis tessmannii</i> Rendle	0.36	0.61	0.03	0.29
<i>Chrysophyllum lacourtianum</i> De Wild.	0.05	0.15		
<i>Chytranthus carneus</i> Radlk.	0.21	0.46		
<i>Cleistanthus mildbraedii</i> Jabl. & J.Leonard	1.24	2.35	0.84	3.76
<i>Clusiaceae spp</i>	0.11	0.46		
<i>Coelocaryon preussii</i> Warb.	0.26	1.07	0.75	0.87
<i>Cola altissima</i> Engl.	0.04	0.31		
<i>Cola gigantea</i> A.Chev.	0.13	0.61		
<i>Cola griseiflora</i> De Wild.	0.53	2.75	1.79	8.24

Appendix 2 - Continued

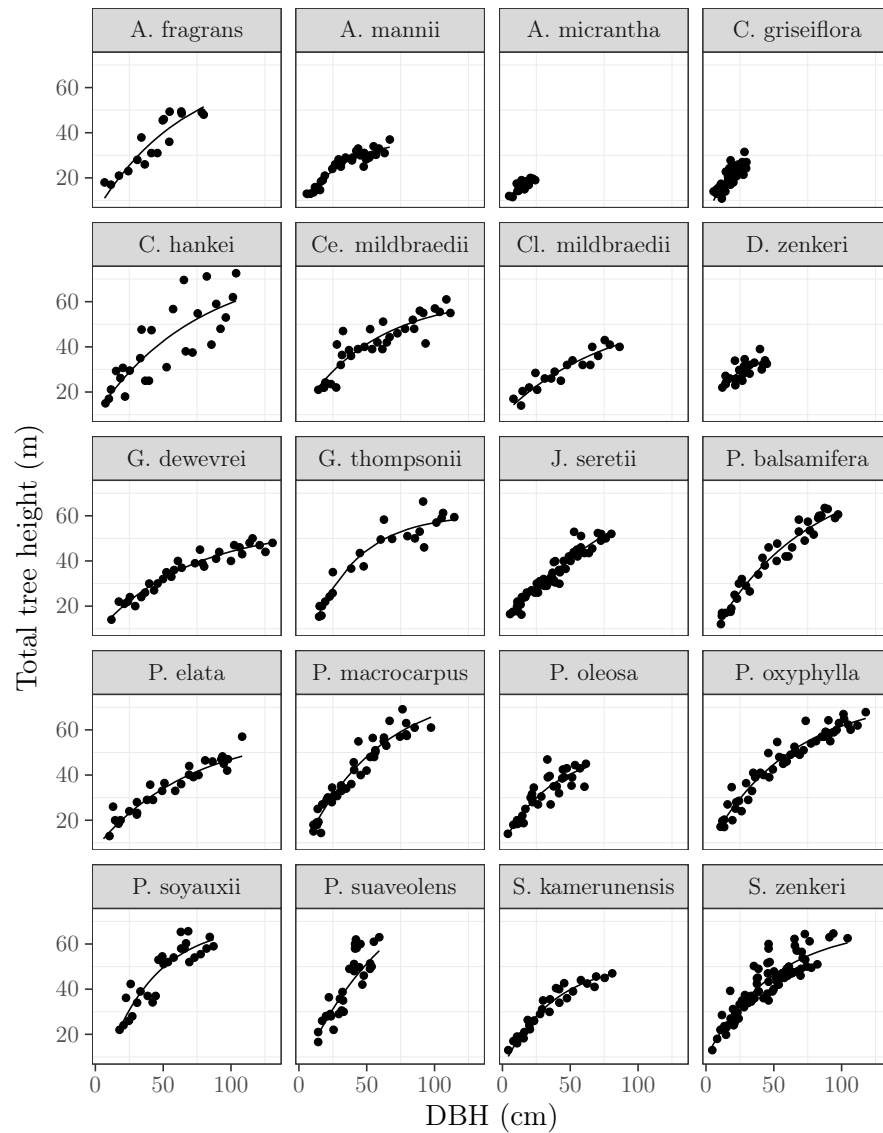
Sp	MIF		MOF	
	% BA	% N	% BA	% N
<i>Combretum lokele</i> Liben			0.07	0.39
<i>Cynometra hankei</i> Harms	6.99	3.21	0.08	0.29
<i>Dacryodes yangambiensis</i> Louis ex Troupin	0.08	0.15		
<i>Dialium corbisieri</i>	1.23	1.07	0.08	0.58
<i>Dialium pachyphyllum</i> Harms	0.36	0.61	0.07	0.87
<i>Dialium excelsum</i> Steyaert	0.43	0.19		
<i>Dichostemma glaucescens</i> Pierre	0.03	0.15		
<i>Diogoia zenkeri</i> (Engl.) Exell & Mendonca	0.71	1.53	0.33	1.16
<i>Diospyros crassiflora</i> Hiern	0.08	0.31	0.16	2.64
<i>Diospyros hoyleana</i> F.White	0.12	0.76	0.19	2.33
<i>Diospyros</i> sp			0.08	0.58
<i>Donella pruniformis</i> Pierre	1.99	0.46	0.47	0.58
<i>Drypetes gossweileri</i> S.Moore	0.49	0.46	0.18	1.55
<i>Drypetes likwa</i> J. Leonard.	0.91	3.36	0.03	0.29
<i>Drypetes</i> sp	0.04	0.31	0.05	0.29
<i>Drypetes spinosa-dentata</i> Hutch	0.09	0.15		
<i>Entandrophragma candollei</i> Harms	0.24	0.46	0.06	0.29
<i>Entandrophragma cylindricum</i> Sprague	0.03	0.15		
<i>Entandrophragma utile</i> (Dawe & Sprague)	1.35	0.31		
<i>Garcinia epunctata</i> Stapf	0.22	0.46	0.05	0.29
<i>Gilbertiodendron dewevrei</i> (De Wild.) J.Leonard			73.1	34.99
<i>Grewia trinervia</i> De Wild.	0.38	0.76		
<i>Grossera multinervis</i> J.Leonard	1.3	3.36	0.11	0.87
<i>Guarea cedrata</i> (A.Chev.) Pellegr.	1.32	0.76		
<i>Guarea thompsonii</i> Sprague & Hutch.	1.43	4.28		
<i>Heisteria parvifolia</i> Sm.	0.68	1.99	0.13	0.87
<i>Julbernardia seretii</i> (De Wild.) Troupin	4.67	4.13	0.35	2.41
<i>Klainedoxa gabonensis</i> Pierre	0.23	0.33		

Appendix 2 - Continued

Sp	MIF		MOF	
	% BA	% N	% BA	% N
<i>Massularia acuminata</i> (G.Don) Bullock	0.03	0.31	0.03	0.29
<i>Microdesmis yafungana</i> J.Leonard	0.03	0.15		
<i>Monodora angolensis</i> Welw.			0.06	0.87
<i>Monodora myristica</i> (Gaertn.) Dunal			0.09	0.6
<i>Musanga cecropioides</i> R.Br.	0.22	0.31		
<i>Nauclea diderrichii</i> Merr.	1.46	0.31		
<i>Nesogordonia kabingaensis</i> (K.Schum.)	0.66	0.5		
<i>Pancovia harmsiana</i> Gilg	0.3	1.83		
<i>Pancovia laurentii</i> De Wild.	0.04	0.15		
<i>Panda oleosa</i> Pierre	2.01	2.45	1.57	1.16
<i>Pentaclethra macrophylla</i> Benth.	0.04	0.15	0.28	0.58
<i>Pericopsis elata</i> (Harms) Breteler	1.12	0.39		
<i>Petersianthus macrocarpus</i> (P.Beauv.) Liben	3.78	1.43		
<i>Phyllocosmus africanus</i> (Hook.f.) Klotzsch	0.03	0.15	0.06	1.45
<i>Polyalthia suaveolens</i> Engl. & Diels	2.93	5.86	0.97	2.6
<i>Pouteria aningeri</i> Baehni	0.02	0.15	0.08	0.87
<i>Prioria balsamifera</i> (Vermoesen) Breteler	2.89	1.53	0.28	0.58
<i>Prioria oxyphylla</i> (Harms) Breteler	4.62	1.07	6.04	2.05
<i>Pterocarpus soyauxii</i> Taub.	2.53	1.22	0.05	0.29
<i>Pycnanthus angolensis</i> (Welw.) Warb.	0.52	1.83	0.01	0.29
<i>Quassia undulata</i> (Guill. & Perr.) D.Dietr.	0.05	0.41		
<i>Rinorea oblongifolia</i> (C.H.Wright)	0.16	0.92		
<i>Rothmannia lujae</i> (De Wild.) Keay			0.13	1.73
<i>Sapotaceae</i> sp	0.03	0.15		
<i>Scorodophloeus zenkeri</i> Harms	28.23	12.47	7.81	5.49
<i>Staudtia kamerunensis</i> Warb.	0.86	4.28	0.48	3.18
<i>Sterculia africana</i> (Lour.) Fiori	0.28	0.31		
<i>Strombosia pustulata</i> Oliv.	0.03	0.15	0.07	0.3
<i>Strombosiopsis tetrandra</i> Engl.	0.15	0.61	0.11	0.6

Appendix 2 - Continued

Sp	MIF		MOF	
	% BA	% N	% BA	% N
<i>Synsepalum subcordatum</i> De Wild.	0.05	0.31	0.11	0.6
<i>Tessmannia africana</i> Harms	2.32	0.61	0.14	0.3
<i>Treculia africana</i> Decne.	0.05	0.15		
<i>Trichilia gilgiana</i> Harms	1.02	2.6	0.09	0.58
<i>Trichilia prieureana</i> A.Juss.	0.92	2.45		
<i>Trichilia</i> sp	0.06	0.46		
<i>Tridesmostemon omphalocarpoides</i> Engl.	0.02	0.15		
<i>Trilepisium madagascariense</i> DC.	0.03	0.31		
<i>Turraeanthus africanus</i> (Welw. ex C.DC.)	0.85	1.63		
<i>Vitex congolensis</i> De Wild. & T.Durand	0.02	0.15		
<i>Xylia ghesquierei</i> Robyns & Robyns	0.07	0.15		



Appendix 3 – Observed (dots) and predicted (solid lines) tree height vs. DBH relationships for the different species sampled in the Yoko Forest Reserve. The parameter estimates of the three-parameters exponential model $H = a - b e^{(-c \text{ DBH})}$ are given in Appendix 6.

Appendix 4 – List of sampled tree species. Family, scientific name, observed DBH range, number of trees sampled for height allometry and number of trees sampled for wood specific gravity (WSG).

Family	Species	DBH range (cm)	Trees sampled for height	Trees sampled for WSG
Rubiaceae	<i>Aidia micrantha</i> (K.Schum.) F.White	10-24	18	9
Annonaceae	<i>Anonidium mannii</i> (Oliv.) Engl. & Diels	10-67	32	12
Fabaceae	<i>Anthonothea fragrans</i> (Baker f.) Exell & Hillc.	10-80	17	4
Cannabaceae	<i>Celtis mildbraedii</i> Engl.	10-112	32	7
Phyllanthaceae	<i>Cleistanthus mildbraedii</i> Jabl. & J.Leonard	10-86	19	5
Malvaceae	<i>Cola griseiflora</i> De Wild.	10-30	37	12
Fabaceae	<i>Cynometra hankei</i> Harms	10-104	27	8
Olacaceae	<i>Diogoia zenkeri</i> (Engl.) Exell & Mendonca	10-45	28	11
Fabaceae	<i>Gilbertiodendron</i> <i>deweveii</i> (De Wild.) J.Leonard	10-130	38	14
Meliaceae	<i>Guarea thompsonii</i> Sprague & Hutch.	10-115	23	8
Fabaceae	<i>Julbernardia seretii</i> (De Wild.) Troupin	10-80	58	10
Pandaceae	<i>Panda oleosa</i> Pierre	10-62	32	14
Fabaceae	<i>Pericopsis elata</i> (Harms) Meeuwen	10-110	27	12
Lecythidaceae	<i>Petersianthus</i> <i>macrocarpus</i> (P.Beauv.) Liben	10-98	43	9
Annonaceae	<i>Polyalthia suaveolens</i> Engl. & Diels	10-60	27	12
Fabaceae	<i>Prioria balsamifera</i> (Vermoesen) Breteler	10-97	34	10
Fabaceae	<i>Prioria oxyphylla</i> (Harms) Breteler	10-120	52	15
Fabaceae	<i>Pterocarpus soyauxii</i> Taub.	10-87	27	5
Fabaceae	<i>Scorodophloeus zenkeri</i> Harms	10-105	77	18
Myristicaceae	<i>Staudtia kamerunensis</i> Warb.	10-80	29	9

Appendix 5 – Basal area based proportions (BA ratio) of all tree species sampled in the mixed (MIF) and monodominant (MOF) forests in the Yoko reserve.

Species	Basal area ratios (%)	
	MIF	MOF
<i>Aidia micrantha</i> (K.Schum.) F.White	0.59	0.17
<i>Anonidium mannii</i> (Oliv.) Engl. & Diels	2.99	1.02
<i>Anthonotha fragrans</i> (Baker f.) Exell & Hillc.	1.34	0.53
<i>Celtis mildbraedii</i> Engl.	2.31	0
<i>Cleistanthus mildbraedii</i> Jabl. & J.Leonard	1.24	0.84
<i>Cola griseiflora</i> De Wild.	0.52	1.79
<i>Cynometra hankei</i> Harms	6.98	0.08
<i>Diogoia zenkeri</i> (Engl.) Exell & Mendonca	0.71	0.33
<i>Gilbertiodendron dewevrei</i> (De Wild.) J.Leonard	0	73.1
<i>Guarea thompsonii</i> Sprague & Hutch.	1.43	0
<i>Julbernardia seretii</i> (De Wild.) Troupin	4.67	0.35
<i>Panda oleosa</i> Pierre	2.01	1.57
<i>Pericopsis elata</i> (Harms) Meeuwen	1.12	0
<i>Petersianthus macrocarpus</i> (P.Beauv.) Liben	3.78	0
<i>Polyalthia suaveolens</i> Engl. & Diels	2.93	0.97
<i>Prioria balsamifera</i> (Vermoesen) Breteler	2.89	0.28
<i>Prioria oxyphylla</i> (Harms) Breteler	4.62	6.04
<i>Pterocarpus soyauxii</i> Taub.	2.53	0.05
<i>Scorodophloeus zenkeri</i> Harms	28.2	7.81
<i>Staudtia kamerunensis</i> Warb.	0.86	0.48
Total	71.72	95.41

Appendix 6 – total height (H) to diameter at breast height (DBH) for all sampled tree species in the Yoko reserve. Adult stature was defined according to Bénédet et al. [2015]

Species	Adult stature	a	b	c	RSE
<i>Aidia micrantha</i> (K.Schum.) F.White	Small	21.59	15.35	0.081	5.44
<i>Anonidium mannii</i> (Oliv.) Engl. & Diels	Small	37.13	34.58	0.033	0.27
<i>Anthonotha fragrans</i> (Baker f.) Exell & Hillc.	Large	71.83	67.32	0.015	5.19
<i>Celtis mildbraedii</i> Engl.	Large	62.31	52.15	0.018	16.04
<i>Cleistanthus mildbraedii</i> Jabl. & J.Leonard	Medium	56.59	46.97	0.013	4.47
<i>Cola griseiflora</i> De Wild.	Small	34.42	31.85	0.047	0.77
<i>Cynometra hankei</i> Harms	Large	77.26	67.95	0.013	0.14
<i>Diogoa zenkeri</i> (Engl.) Exell & Mendonca	Small	35.16	30.67	0.064	0.7
<i>Gilbertiodendron dewevrei</i> (De Wild.) J.Leonard	Medium	54.92	47.4	0.015	1.44
<i>Guarea thompsonii</i> Sprague & Hutch.	Medium	60.74	67.57	0.029	0.28
<i>Julbernardia seretii</i> (De Wild.) Troupin	Large	88.31	77.57	0.01	0.91
<i>Panda oleosa</i> Pierre	Medium	50.97	41.82	0.028	0.02
<i>Pericopsis elata</i> (Harms) Meeuwen	Medium	59.54	51.95	0.014	1.18
<i>Petersianthus macrocarpus</i> (P.Beauv.) Liben	Large	78.47	75.18	0.018	1.25
<i>Polyalthia suaveolens</i> Engl. & Diels	Large	97.36	95.14	0.014	0.73
<i>Prioria balsamifera</i> (Vermoesen) Breteler	Large	81.28	78.47	0.014	0.68
<i>Prioria oxyphylla</i> (Harms) Breteler	Large	75.09	68.55	0.016	10.46
<i>Pterocarpus soyauxii</i> Taub.	Large	69.12	75.75	0.027	13.33
<i>Scorodophloeus zenkeri</i> Harms	Medium	67.84	58.15	0.02	0.48
<i>Staudtia kamerunensis</i> Warb.	Medium	52.03	46.92	0.027	0.19

Appendix 7 – Statistics (number of observations, N; average $\pm$ standard deviation; range) for all potential explanatory variables of upper soil C stocks within the mixed (MIF) and monodominant (MOF) forests, as used in linear regressions (Table 4). The p-values relate to the difference between forest types.

Variables	Forest types						p-value
	MIF			MOF			
	N	Average $\pm$ sd	Range (min-max)	N	Average $\pm$ sd	Range (min-max)	
Litter quantity							
C inputs as foliar litterfall (Mg C year ⁻¹ ha ⁻¹)	72	2.71 $\pm$ 0.49	1.93-4.47	32	2.75 $\pm$ 0.44	1.91-3.62	0.82
Litter quality							
CN ratio	22	15.94 $\pm$ 1.90	10.29-19.67	20	24.49 $\pm$ 2.58	20.63-28.36	< 0.01
CP ratio	22	421.9 $\pm$ 114.8	200.7-684.7	20	1025.4 $\pm$ 362.1	602.4-2213.4	0.02
CS ratio	22	91.2 $\pm$ 37.3	38.0-166.0	20	270.1 $\pm$ 108.9	76.9-511.1	0.03
NP ratio	22	26.5 $\pm$ 7.0	16.2-42.6	20	41.7 $\pm$ 13.5	27.3-86.6	0.06
PCA 1	22	2.10 $\pm$ 1.54	0.12-6.94	20	-2.57 $\pm$ 1.33	-5.97- -0.59	< 0.01
PCA 2	22	0.21 $\pm$ 1.04	-1.83-1.71	20	-0.26 $\pm$ 1.05	-2.17-1.43	0.49
Stand parameters							
Total BA (m ² ha ⁻¹)	72	30.36 $\pm$ 10.82	9.19-62.27	32	25.23 $\pm$ 11.03	6.85-45.66	0.42
Dominant tree species BA ratio	72	0.26 $\pm$ 0.19	0.00-0.74	32	0.67 $\pm$ 0.22	0.13-0.97	ND
Dominant tree species BA (m ² ha ⁻¹)	72	7.74 $\pm$ 6.23	0.00-26.62	32	18.78 $\pm$ 12.47	2.59-40.39	ND
Shannon div. index	72	1.81 $\pm$ 0.31	1.04-2.47	32	0.96 $\pm$ 0.55	0.16-2.34	< 0.01
Soil parameters							
pH CaCl ₂ 0-10 cm	72	3.70 $\pm$ 0.09	3.50-3.95	32	3.39 $\pm$ 0.10	3.15-3.60	< 0.01
CN ratio 0-10 cm	72	12.44 $\pm$ 0.96	9.21-14.74	32	15.09 $\pm$ 1.06	13.53-18.04	< 0.01

Appendix 8 – Pearson correlation coefficients between 11 leaf litter traits of litterfall in MIF (a.) and MOF (b.). *, **, *** denote a significant correlation at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$.

a. MIF											
Trait											
Trait	P	Mg	Mn	K	Ca	S	Si	NP.ratio	CN.ratio	CP.ratio	
Mg	0.66***										
Mn	0.83***	0.61**									
K	0.77***	0.51*	0.67***								
Ca	0.58**	0.76***	0.61**	0.58**							
S	0.44*	0.16	0.21	0.07	-0.01						
Si	0.12	0.15	0.29	-0.12	0.37	-0.08					
NP.ratio	-0.83***	-0.31	-0.66***	-0.61**	-0.19	-0.42	-0.03				
CN.ratio	-0.4	-0.66***	-0.38	-0.15	-0.67**	-0.37	-0.33	-0.09			
CP.ratio	-0.95***	-0.55**	-0.78***	-0.62**	-0.42	-0.53*	-0.17	0.91***	0.32		
CS.ratio	-0.56***	-0.31	-0.36	-0.17	-0.08	-0.91***	0.00	0.55**	0.37	0.67***	
b. MOF											
Trait											
Mg	0.71**										
Mn	0.63**	0.66**									
K	0.68**	0.72***	0.28								
Ca	0.22	0.42*	0.28	0.29							
S	0.67**	0.49*	0.76***	0.15	0.09						
Si	0.34	0.38	0.03	0.50*	0.52*	0.06					
NP.ratio	-0.83***	-0.50*	-0.34	-0.58*	-0.31	-0.46*	-0.50*				
CN.ratio	-0.49*	-0.37	-0.50*	-0.18	0.03	-0.52*	0.28	0.11			
CP.ratio	-0.89***	-0.56*	-0.43	-0.60**	-0.30	-0.55*	-0.38	0.96***	0.38		
CS.ratio	-0.82***	-0.62**	-0.66***	-0.38	-0.33	-0.84***	-0.39	0.78***	0.39	0.82***	

Appendix 9 – Mean leaf litter traits of *Scorodophloeus zenkeri* Harms and *Gilbertiodendron dewevrei* (De Wild.) J.Leonard

Litter traits	Species	
	<i>S. zenkeri</i>	<i>G. dewevrei</i>
C (%)	47.39	49.05
N (%)	3.06	1.45
Ca (g.kg ⁻¹)	14.01	5.43
K (g.kg ⁻¹)	7.65	4.02
Mg (g.kg ⁻¹)	3.21	2.18
Mn (g.kg ⁻¹)	3.5	0.03
P (g.kg ⁻¹)	1.52	0.56
S (g.kg ⁻¹)	9.72	1.27
Si (g.kg ⁻¹)	17.45	24.44
CN ratio	15.45	33.82
CP ratio	312.81	874.66
CS ratio	48.78	385.2
NP ratio	20.25	25.86

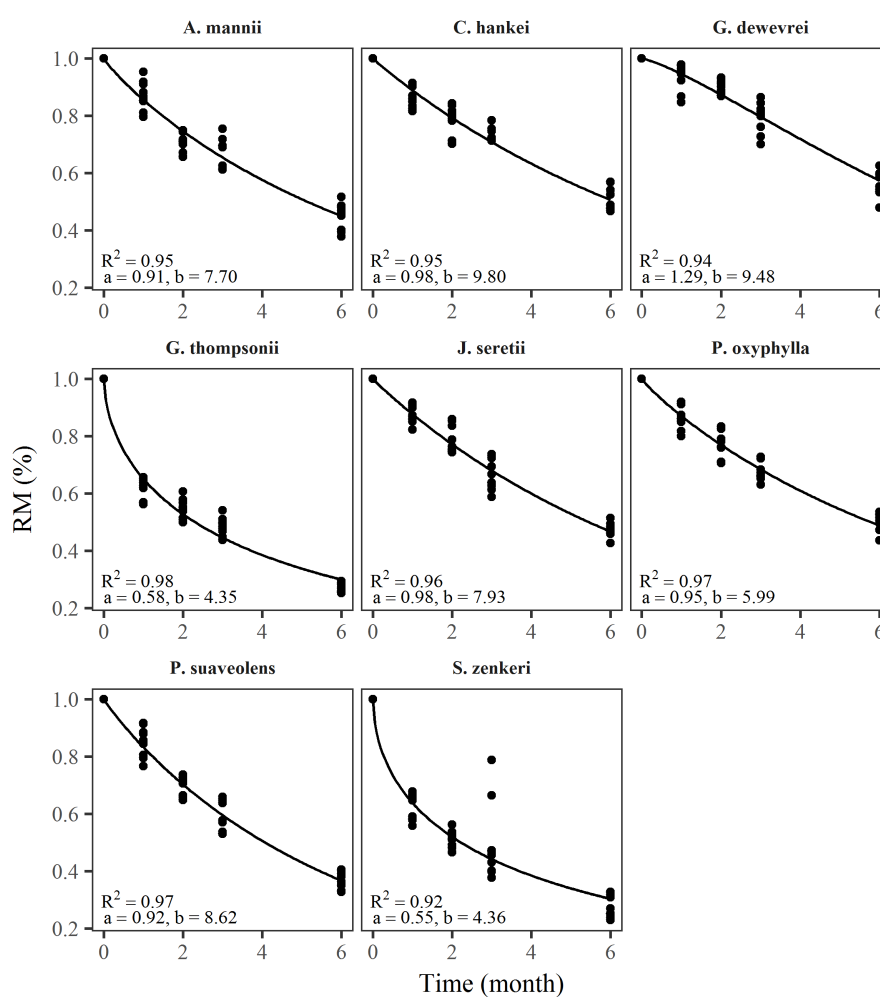
Appendix 10 – Parameter estimates of linear regression models ($Y = a + bX$) relating organic C stocks of upper soil layers (Y, Mg C ha⁻¹) to potential explanatory variables (X) within the mixed (MIF) or monodominant (MOF) forest. FF: forest floor, MS: mineral soil. *, **, *** denote a significant parameter at $p \leq 0.10$, $p \leq 0.05$ and $p \leq 0.01$.

Variables	Forest	FF				MS				FF + MS	
		O _L		O _H +O _F		0-10 cm		10-25 cm		O _L +O _F +O _H + 0-25 cm	
		a	b	a	b	a	b	a	b	a	b
Litter quantity											
C inputs as foliar litterfall (Mg C year ⁻¹ ha ⁻¹)	MIF	0.48	0.16**	1.11**	0.06	7.30***	0.67	8.30***	0.59	17.63***	1.32
	MOF	0.55	0.09	6.49***	-0.41	15.98**	1.16	15.03**	0.51	37.44**	1.67
Litter quality											
CN ratio	MIF	1.25*	-0.02	1.31	0.00	9.81***	-0.04	11.36***	-0.10	22.79***	-0.10
	MOF	-0.59	0.06**	8.77**	-0.16	19.44*	-0.05	9.21	0.29	28.88	0.44
CP ratio	MIF	0.77*	0.00	1.61***	0.00	7.40***	0.00	8.87***	0.00	19.08***	0.01
	MOF	0.76***	0.00	5.94***	0.00	20.71***	0.00	16.66***	0.00	42.71***	0.00
CS ratio	MIF	0.57**	0.01*	1.72***	0.00	7.62***	0.02	9.03***	0.01	19.13***	0.03
	MOF	0.69***	0.00	5.35***	0.00	17.97***	0.00	13.61***	0.01	34.52***	0.02
NP ratio	MIF	0.76*	0.01	1.62***	-0.01	7.21***	0.07	8.48***	0.05	18.76***	0.10
	MOF	0.87**	0.00	5.61***	-0.01	20.78***	-0.06	17.32***	-0.03	43.52***	-0.10
PCA 1	MIF	1.03***	-0.03	1.16***	0.08	9.35***	-0.22	9.71***	-0.05	21.39***	-0.21
	MOF	0.71***	-0.04	5.42***	0.18	18.64***	0.19	15.30***	-0.35	38.30***	-0.51
PCA 2	MIF	1.00**	-0.17*	1.36***	-0.10	8.89***	-0.15	9.77***	-0.73*	21.11***	-1.03
	MOF	0.82***	-0.03	4.90***	-0.12	18.22***	0.27	16.56***	1.39	40.07***	1.40
Stand parameters											
Total BA (m ² ha ⁻¹)	MIF	1.01***	0.00	1.04***	0.01	7.69***	0.05**	8.67***	0.05**	18.45***	0.10**
	MOF	0.81***	0.00	5.18***	0.01	15.25***	0.16	16.72***	-0.01	38.57***	0.13
Dominant tree species BA ratio	MIF	0.88***	0.00	1.27***	0.00	8.29***	0.11**	9.25***	0.09**	19.52***	0.21***
	MOF	0.82***	0.00	4.99***	0.02	15.99***	0.16*	16.27***	0.01	38.42***	0.19
Dominant tree species BA (m ² ha ⁻¹)	MIF	0.88***	0.11	1.32***	-0.16	8.65***	1.81	9.68**	0.87*	20.25***	3.50
	MOF	0.87***	-0.10	3.83***	2.17*	13.05***	9.07*	17.48***	-1.57	36.83***	7.57
Shannon div. index (SI)	MIF	1.28***	-0.20	0.67*	0.33	12.95***	-2.11***	12.52***	-1.43**	27.93***	-3.74***
	MOF	0.79***	0.02	5.76***	-0.45	21.91***	-2.85	15.83***	0.63	43.79***	-1.86
Soil parameters											
pH CaCl ₂ 0-10 cm	MIF	3.57**	-0.72*	1.63	0.00	63.11***	-14.68***	38.99***	-7.90***	110.83***	-24.37***
	MOF	-0.28	0.32	6.41**	0.00	199.33***	-53.08***	93.48***	-22.71**	321.74***	-82.52***
CN ratio 0-10 cm	MIF	-0.80*	0.14***	1.52*	-0.02	-8.73***	1.44***	-0.14	0.81***	-8.44*	2.38***
	MOF	0.64	0.01	5.69	-0.02	3.54	1.05	1.31	1.02	6.93	2.33

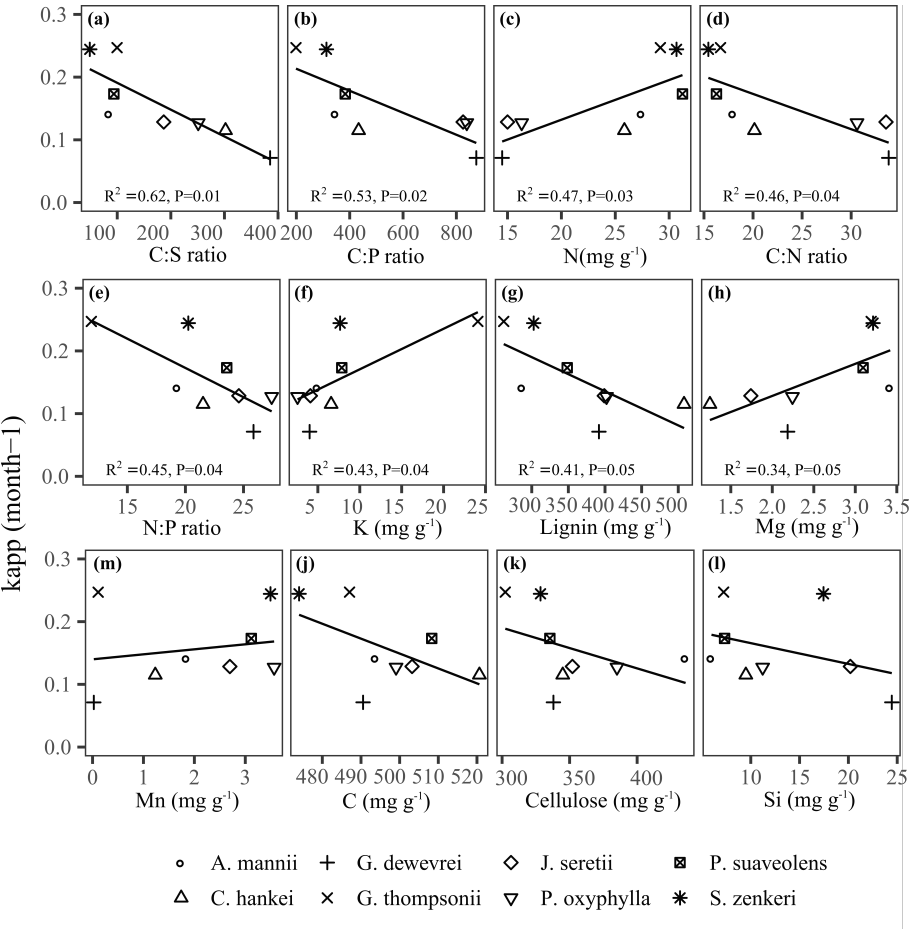
Appendix 11 – Correlations between the 0-10 and 10-25 cm SOC stock, and the clay or silt content in the 0-10 cm soil layer for MIF and MOF in the soil pits.

Depth	Forest	SOC stocks vs. clay content		SOC stocks vs. silt content	
		Coefficient of correlation	p-value	Coefficient of correlation	p-value
0-10 cm	MIF	-0.52	0.37	0.03	0.97
	MOF	0.72	0.27	0.8	0.15
10-25 cm	MIF	-0.82	0.11	0.16	0.8
	MOF	0.5	0.67	0.62	0.37

Appendix 12 – The relative litter biomass remaining at 1, 2, 3 and 6 months for the single-species litterbags of *A. mannii*, *C. hankei*, *G. dewevrei*, *G. thompsonii*, *J. seretii*, *P. suaveolens*, *P. oxyphylla* and *S. zenkeri* under MIF in the Yoko Reserve. The summary and the parameter estimates of the decay rate model $RM = \exp(-(t/b)^a)$ are given in the captions



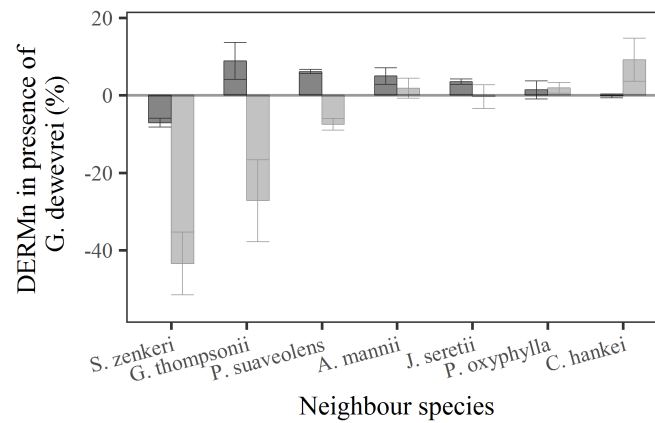
Appendix 13 – Apparent litter decay rates (k) after 1 month of incubation under MIF for 8 tropical tree species as a function of litter S, N, K, lignin and Mg leaf litter concentrations and C:P, C:N and N:P leaf litter ratios in the Yoko Reserve



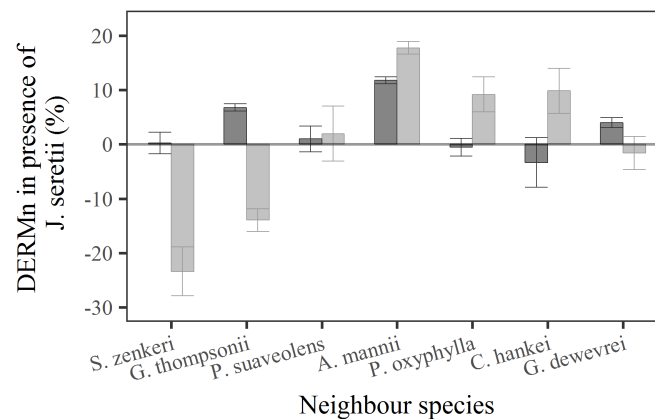
Appendix 14 – Maximum relative decomposition index of the mixture (MRDI_m) under MIF. High MRDI_m indicate the presence of easily decomposable litter in the mixture

Mixture ID	Mixture	MRDI _m (%)	
		t=1	t=6
1	A. mannii + P. suaveolens	0.89	1.07
2	C. hankei + A. mannii	0.90	1.01
3	C. hankei + G. thompsonii	2.21	1.19
4	C. hankei + J. seretii	0.78	0.96
5	C. hankei + P. suaveolens	1.30	1.01
6	C. hankei + P. oxyphylla	0.93	0.97
7	G. dewevrei + A. mannii	0.81	0.99
8	G. dewevrei + C. hankei	0.66	0.96
9	G. dewevrei + G. thompsonii	2.05	1.16
10	G. dewevrei + J. seretii	0.73	0.93
11	G. dewevrei + P. suaveolens	0.95	1.08
12	G. dewevrei + P. oxyphylla	0.72	0.86
13	G. thompsonii + A. mannii	1.72	1.21
14	G. thompsonii + P. suaveolens	1.75	1.26
15	J. seretii + A. mannii	1.09	1.11
16	J. seretii + G. thompsonii	1.99	1.22
17	J. seretii + P. suaveolens	0.78	1.14
18	J. seretii + P. oxyphylla	0.80	1.00
19	P. oxyphylla + A. mannii	0.86	1.05
20	P. oxyphylla + G. thompsonii	1.96	1.20
21	P. oxyphylla + P. suaveolens	0.90	1.06
22	S. zenkeri + A. mannii	1.75	1.19
23	S. zenkeri + C. hankei	1.81	1.13
24	S. zenkeri + G. dewevrei	1.60	1.07
25	S. zenkeri + G. thompsonii	2.04	1.22
26	S. zenkeri + J. seretii	1.81	1.17
27	S. zenkeri + P. suaveolens	1.75	1.20
28	S. zenkeri + P. oxyphylla	1.74	1.13

Appendix 15 – Mean deviation from the expected relative remaining litter mass of the neighbour species in the mixture ($DERM_n$) in the presence of *G. dewevrei* after 1 and 6 months (in black and grey, respectively). Species are ordered according to their k_{app} after 1 month of incubation. Means and SE are shown



Appendix 16 – Mean deviation from the expected relative remaining litter mass of the neighbour species in the mixture ($DERM_n$) in the presence of *J. seretii* after 1 and 6 months (in black and grey, respectively). Species are ordered according to their k_{app} after 1 month of incubation. Means and SE are shown



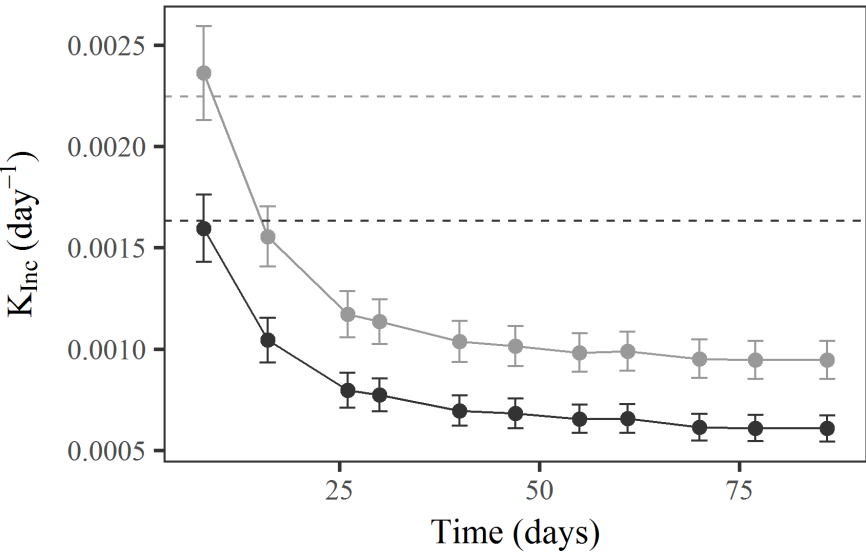
Appendix 17 – Distribution of the 106 plots set up in MIF and MOF between the four types of cluster. A cluster is made of three mature canopy trees forming a triangle with the trees ranging 2.5-9.3 m from the centre of the cluster (Figure R:ClusterScheme)

Type of cluster	MIF		MOF	
	<i>S. zenkeri</i>	N	<i>G. dewevrei</i>	N
Monospecific	With	16	With	13
Two-species	With	23	With	16
Three-species	With	21	NA	NA
	Without	17	NA	NA
Total		77		29

Appendix 18 – Parameter estimates (mean $\pm$ standard error) for the semi-empirical model of soil respiration (Eq. 4.4). $R^2=0.54$, $p<10^{-5}$. *, **, *** denote a significant coefficient at $p\leq 0.05$, $p\leq 0.01$ and $p\leq 0.001$, respectively.

Model terms	MIF	MOF
a		$-3.26 \pm 0.36^{***}$
b	$14.04 \pm 0.58^{***}$	$14.33 \pm 0.55^{***}$

Appendix 19 – Decay rate of the 0-10 cm mineral soil layer (K_{inc} , $\text{gC-CO}_2 \text{ gCsoil}^{-1} \text{ day}^{-1}$) estimated from a laboratory incubation experiment using soils from mixed (MIF, in gray) and monodominant (MOF, in black) forests. Averages $\pm$ standard errors. Dotted lines represent k_{MS} of the 0-10 cm layer fitted using equations 4.1 to 4.3 with a mixed procedure where the random plot and date of measurement effects are nested within forest type (cf. Table 4.4)



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Publications

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