Nutrient cycling of Bornean tropical forests

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List of acronyms

BB	Branch bottom
BM	Branch middle
BT	Branch top
C	Carbon
Ca	Calcium
CR	Coarse root
DBH	Diameter at Breast Height
GEM	Global Ecosystem Monitoring network
GPP	Gross primary productivity
K	Potassium
LES	Leaf Economics Spectrum
Mg	Magnesium
N	Nitrogen
NPP	Net primary productivity
P	Phosphorus
SAFE	Stability of Altered Forest Ecosystems Project
SE	Standard error
TB	Trunk bottom
TM	Trunk middle
TT	Trunk top
WD	Wood density
WES	Wood Economics Spectrum

Chapter 1

Abstract

The thesis addresses a novel topic of nutrient cycling of tropical forests and substantially adds to the small amount of currently available data in the area. While nutrients like nitrogen (N) and phosphorus (P) are considered to limit net primary productivity (NPP) in lowland tropical forests, direct evidence of nutrient limitation of NPP is scarce.

The thesis focuses on humid lowland tropical forests along a disturbance gradient in Malaysian Borneo and quantifies key biological processes of nutrient cycling: nutrient requirement, uptake, use efficiency, resorption and allocation. The first empirical chapter examines wood-specific nutrient concentrations and their radial and vertical allocation within a whole tree. The second and third empirical chapters examine the effects of logging disturbance and soil availability on net primary productivity and nutrient cycling. Five macronutrients of N, P, potassium (K), calcium (Ca), magnesium (Mg), and carbon (C) are considered. I developed and employed a novel approach of coupling data on nutrient stoichiometry and NPP to provide direct estimates of fluxes and allocation of nutrients within forest ecosystems.

In logged forests, the contribution of leaf resorption towards meeting nutrient requirement and the allocation of nutrients to canopy were lower, while allocation of nutrients to wood was higher than in old-growth forest. Contrary to expectation, NPP did not correlate with soil nutrient availability of any elements, suggesting soil

availability is a weak predictor of NPP. Depending on the nutrient, different strategies, such as changes in resorption rates and changes in nutrient use efficiency, were adopted to compensate for low supply of that nutrient. Overall, this study demonstrates the value of coupling NPP with stochiometric data to gain insights into the nutrient cycle of intact and disturbed forests. These insights explain how limited supply of P, K and Ca is a challenge in lowland tropical forest ecosystems.

The study found higher concentrations in sapwood relative to heartwood for Dipterocarp species, which provide empirical support for wood resorption during sapwood senescence. It also showed exceptionally high nutrient concentrations in the bark, which suggest debarking during logging operations could substantially contribute to maintaining nutrients within forest ecosystems.

Declaration

I composed this thesis; the work is my own, except where otherwise acknowledged. No part of this thesis has been submitted for any other degree or qualification.

Takeshi Inagawa

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Chapter 1 Introduction

1.1 Background

Knowledge gap in nutrients

Nutrient availability constrains key ecosystem processes, such as net primary productivity (NPP), plant nutrient uptake and nutrient use efficiency across all ecosystems. Nitrogen (N) and phosphorus (P), either individually or in combination, are considered to limit primary productivity in most terrestrial ecosystems including tropical forests (Herbert et al., 2003, Aragão et al., 2009, Quesada et al., 2009, Chave et al., 2010, Vitousek et al., 2010, Vitousek and Howarth, 1991). As a result, plant adaptations to limitation of these nutrients constrain ecosystem rates of nutrient cycling (Chapin, 1980, Vitousek, 2004, Hobbie, 1992).

While soils of most lowland tropical forests are highly weathered and P-depleted, N is relatively abundant due to biological fixation (Walker and Syers, 1976, Vitousek and Farrington, 1997). As a result, tropical forests are considered to be P limited. A wide range of studies document that tree growth and NPP are mainly constrained by soil P availability in tropical forests (Vitousek and Sanford, 1986, Crews et al., 1995, Herbert and Fownes, 1995, Sollins, 1998, Tiessen, 1998, Cleveland et al., 2002).

Tropical forests only cover about 10% of Earth's land surface, but they account for 34% of terrestrial net primary production (NPP) and hold about 25% of the terrestrial biomass carbon (C) (Lewis et al., 2009, Malhi, 2012). They are also estimated to

account for nearly 70% of terrestrial N fixation (Wang and Houlton, 2009). Yet it is not well understood how nutrients constrain tropical C cycle due to an overall lack of nutrient data in the tropics.

Previous nutrient studies have been conducted mostly in undisturbed forest ecosystems. Only 30% of the existing tropical forest area is relatively undisturbed or intact (Potapov et al., 2008), whereas the remaining area has been disturbed mostly through selective logging, which underlines the necessity of understanding nutrient dynamics in secondary growth forests (McGrath et al., 2001, Gomes and Luizao, 2012). While the majority of studies in disturbed and secondary forests have focused on Amazonia (Johnson et al., 2001, Feldpausch et al., 2004, Markewitz et al., 2004, Davidson et al., 2007, Gomes and Luizao, 2012), little emphasis has been put in Southeast Asia. Malaysian Borneo (states of Sabah and Sarawak) is one of the global hotspots of such disturbance such as deforestation and forest degradation (Fisher et al., 2011).

Several studies identify nutrient cycling in tropical forests as a knowledge gap, highlighting the urgent need for further nutrient studies, particularly in relation to carbon cycling and global climate change. The thesis provides insights into unknown or poorly known areas of nutrient cycling along disturbance and soil availability gradients.

1.2 Aims

The overall aim of the thesis is to describe the key processes of nutrient cycling

(requirement, uptake, resorption, use efficiency, uptake efficiency and allocation), and how wood macronutrient concentrations vary radially and along the length of a tree in Bornean tropical forest ecosystems.

There are three key research questions in the thesis, which form the themes of Chapter 4 to 7:

1. How do wood nutrients and wood density vary vertically and radially within trees?
2. How do nutrient uptake, use efficiency, resorption and allocation vary along a disturbance gradient from intact to moderately and heavily logged forests?
3. How do net primary productivity (NPP) and nutrient budgets relate to soil nutrient status and uptake?

1.3 Thesis outline

Chapter 1 presents the overall aim of the thesis and the key research questions, which form the themes of *Chapter 4 to 7*, prepared for the submission to peer-review scientific journals. *Chapter 2* identifies key research gaps from a literature review, which highlights the paucity of studies on nutrient cycling in Bornean tropical forests. *Chapter 3* describes the study sites and methods used throughout the thesis. Lastly, *Chapter 7* summarises key research findings throughout the thesis and identifies broad implications and future research recommendations, followed by concluding remarks.

A brief introduction to Chapters 4 to 6 is provided below. Chapters 4 to 6 are all independent but interlinked studies which substantially increase the knowledge on nutrient cycling in tropical forests.

Chapter 4: Vertical and radial variation of wood nutrients and wood density in Bornean tropical forest trees

Chapter 4 reports how wood macronutrient concentrations vary radially and along the length of a tree for 10 tropical tree species in Sabah, Malaysia. To our knowledge, this is the first detailed quantification of nutrient allocation across woody components in the tropical forests, considering vertical and radial variation within a whole tree.

Research questions:

Q1) How do wood nutrient concentrations vary within a trunk cross-section (radially)?

Q2) Is there evidence for nutrient resorption or accumulation in wood during sapwood senescence?

Q3) How do wood nutrient concentrations vary along the length of the tree (vertically)?

Q4) How does wood density vary vertically, and how does it correlate with wood nutrient concentration and total tree height?

Chapter 5: Nutrient uptake, resorption and allocation along a disturbance gradient in Bornean tropical forests

The chapter examines key processes of nutrient cycling such as nutrient uptake, use efficiency, resorption and allocation and how they vary along a logging disturbance gradient. It is the first study to provide estimates of nutrient resorption for five macro-nutrients (N, P, K, Ca, Mg).

Research questions:

Q1) What are the rates of leaf nutrient resorption, and how do they vary along a logging disturbance gradient and among plots, and how much do they contribute to plant nutrient requirement?

Q2) How do nutrient requirement, nutrient uptake and nutrient use efficiency vary along a logging disturbance gradient?

Q3) How does the requirement for nutrients vary among organs (leaf, wood and fine root) in ecosystems, and how is the total requirement and soil uptake for new nutrients partitioned between organs?

Chapter 6: Soil nutrient status does not predict tropical forest productivity because of contrasting nutrient strategies: novel insights from a whole ecosystem nutrient budget approach

The overall aim is to examine the relationships between ecosystem nutrient budgets, and net primary productivity and soil nutrient content in old-growth and logged forests in Malaysian Borneo.

Research questions:

Q1) How does NPP vary with soil nutrient content in intact and logged tropical rainforests?

Q2) How does nutrient uptake rate vary with soil nutrient content?

Q3) How does the contribution of resorption to nutrient requirement vary with nutrient uptake rate?

Q4) How does nutrient use efficiency vary with nutrient uptake rate?

Q5) Can allocation shifts to wood explain how NPP is maintained in nutrient-poor sites?

Publication Status of Chapters

Chapter	Status	Journal
4	Ready for submission	*Biotropica*
5	Ready for submission	*Global Change Biology*
6	Ready for submission	

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Chapter 2 Literature review

This chapter introduces nutrient limitation on net primary productivity (NPP), the key biological processes of nutrient cycling, reviews the knowledge on nutrient limitation (particularly phosphorus limitation) in tropical forests, and then identifies research gaps on these in relation to Bornean tropical forests and logging disturbance (also reviews Nutrient stocks in logged forests over time). In addition, nutrient allocation to woody components is reviewed, which is specific to Chapter 4.

2.1 Net primary productivity and nutrients

Tropical forests commonly appear on strongly weathered soils depleted in rock-derived nutrients such as phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). As a result, productivity of tropical forests is considered to be limited by the availability of one or more soil nutrients (Vitousek, 1984, Tanner et al., 1998, Wright et al., 2011).

Yet it is not well understood how nutrients constrain tropical carbon (C) cycle due to an overall lack of nutrient data in the tropics. Both nitrogen (N) and P play important roles in biochemical fixation of CO_2 as N-rich compounds such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Field and Mooney, 1986), and P as a principal component of nucleic acids, sugar phosphates, ATP and phospholipids (Bieleski,

1973). Multiple nutrients such as N and P and probably several other elements are considered to limit tropical C cycle, although only single-element limitation is generally incorporated into C cycle models, resulting in a critical knowledge gap in the capacity to predict the effects of climate change (Townsend et al., 2011). Potassium is also likely to limit NPP, the full range of nutrients that may limit NPP in lowland tropical forests should be considered (Wright et al., 2011).

Nutrient limitation is key to predicting how the tropical C-cycle will respond to climate change (Townsend et al., 2011). Provided that climate change is likely to increase seasonality and variability of tropical rainfall (Malhi et al., 2009), understanding of how nutrient dynamics responds to such a change is imperative. Under various climate scenarios, tropical N inputs may decline due to increasing temperature, and subsequently C balance would change in the future (Wang and Houlton, 2009). It is also questionable whether there would be rapid decomposition and recycling, and more active root foraging, that lead to an increase in NPP (Malhi, 2012).

Climate change plays a role in altering nutrient supply, which in turn could affect NPP of tropical forests in the future. Wang and Houlton (2009) suggest that tropical N inputs via N fixation may decline under various climate change scenarios. Climate change may directly impact nutrient cycling through altering precipitation regime (Chang et al., 2017). For example, soil organic P accumulation may be enhanced by a long-term rainfall increase in the wet season, which in turn reduce soil P availability for plant uptake in tropical forests (Sun et al., 2020).

In the context of Malaysian Borneo, P is likely to be a major limiting element for NPP due to logging (Imai et al., 2012a, Swinfield et al., 2020). The limitation of long-term P could constrain how tropical forests response to rising CO_2 due to decreasing transpiration ratios (Cernusak et al., 2011). Nevertheless, the interaction between CO_2 and P in constraining tropical plant growth remains poorly understood (Cernusak et al., 2013).

2.2 Nutrient limitation in tropical forests

From forest productivity to soil fertility, nutrient cycling and limitation are essential part of ecosystem ecology (Chapin et al., 1986, Vitousek, 2004). Nutrient limitation historically refers to the perspective of Liebig's Law of the Minimum, which states the availability of one or more elements constrains the plant growth relative to demand (Chapin et al., 1987, Gleeson and Tilman, 1992, Danger et al., 2008, Harpole et al., 2011). A balance between inputs, outputs, and organismal demand determines nutrient limitation (Townsend et al., 2011). The potential for nutrient limitation reflects the adaptation of plants to the local balance of nutrient supply and loss (Wright et al., 2011).

The balance of nutrient supply and loss changes as soils age. The most common soil orders in lowland tropics are Ultisols and Oxisols (Sanchez et al., 1982), which are

strongly weathered, and depleted of rock-derived nutrients such as phosphorus (P) due to long periods of leaching and strong adsorption or occlusion of P with iron, aluminum oxides and calcium phosphates (Walker and Syers, 1976, Baillie, 1996, Vitousek and Farrington, 1997). As a result, lowland tropical forests show high rates of foliar P resorption, low litter and foliar P content, and high foliar N:P ratios (Vitousek and Sanford, 1986, McGroddy et al., 2004, Townsend et al., 2007).

In highly weathered soils of most lowland tropical forests, P availability is typically considered to limit NPP (Vitousek, 1984, Chadwick et al., 1999, Porder et al., 2007, Lambers et al., 2008, Hedin et al., 2009, Vitousek et al., 2010), as originally evidenced by the comparisons of litterfall between temperate and tropical forests, highlighting P that distinguishes the stoichiometry (Vitousek, 1984). Recent correlative studies also support low soil P availability constraining NPP (Aragão et al., 2009, Quesada et al., 2009, Chave et al., 2010). Although some studies have demonstrated P limitation of both NPP and decomposition (Vitousek, 2004, Cleveland et al., 2006), direct measurements of nutrient-C interactions in the tropics remain scarce (Townsend et al., 2011).

In lowland tropical forests, it is widely hypothesised that soil N is available in excess of plant demand (Vitousek, 1984, Vitousek and Sanford, 1986, Hedin et al., 2009). Unlike P, the accrual of N via atmospheric deposition for millions of years has contributed to high N availability in tropical forests (Chadwick et al., 1999). Furthermore, leguminous trees are capable of enhancing N availability because of

their symbioses of N-fixing bacteria, which are found throughout the tropics (Crews, 1999, Hedin et al., 2009).

Foliar and soil δ^{15} N measurements also suggest that N is relatively abundant (Martinelli et al., 1999, Ometto et al., 2006, Davidson et al., 2007). A cross-biome analysis suggests that the relationship between leaf photosynthesis capacity and foliar N is constrained by low foliar P (Reich et al., 2009). In Amazonia, variations in stem wood production and basal are growth are explained by P rather than N (Mercado et al., 2011).

Under the P limitation paradigm, plants are likely to have lower tissue P concentrations, or cycle P more efficiently through higher P resorption efficiency (Dalling et al., 2016). It is documented that the N:P ratios of both green and senesced leaves and the difference between these two ratios increase from high latitudes towards the tropics, resulting from low soil P in tropical forests (McGroddy et al., 2004, Kerkhoff et al., 2005). The pattern explains disproportionally efficient P resorption relative to N, and indicates an effective adaptation to P-poor soils (Richardson et al., 2008).

Nevertheless, the generalisation of P limitation may not be applied to the tropics as a whole due to its heterogeneity of soil orders and climate (Townsend et al., 2008). For instance, N limitation is widespread in tropical montane forests, where soils are generally younger and less strongly weathered (Tanner et al., 1998, Adamek et al., 2009). Previous fertilisation experiments in Hawaii show that N is limiting NPP on

young substrates (Vitousek et al., 1993, Herbert and Fownes, 1995, Vitousek and Farrington, 1997, Harrington et al., 2001). In addition, calcium (Ca) (Cuevas and Medina, 1988, Paoli and Curran, 2007) and potassium (K) (Kaspari et al., 2008) may be equally or more limited than P. Nutrient inputs via atmospheric deposition (Chadwick et al., 1999) or the exposure of weathering source material by soil erosion (Porder et al., 2007) is likely to determine variation in the availability of limiting nutrients.

Tropical forests show varying responses to P fertilisation experiments, indicating spatial and temporal heterogeneity in P limitation. While P addition increases diameter growth in Hawaii (Vitousek and Farrington, 1997) and a young secondary forest in Mexico (Campo and Vazquez-Yanes, 2004), a young secondary forest in Brazil shows no significant effect on tree growth (Davidson et al., 2004). In old-growth forests in Kalimantan, Cameroon and Panama, NPP also does not respond significantly to P fertlisation (Mirmanto et al., 1999, Newbery et al., 2002, Wright et al., 2011). In a recent study in Costa Rica, NPP also does not strongly respond to either N or P fertilisation in the short term (Alvarez-Clare et al., 2013), probably due to co-limitation by a nutrient other than N or P, i.e. K, Ca or a combination of macronutrients (Herbert and Fownes, 1995, Kaspari et al., 2008, Townsend et al., 2011, Wright et al., 2011, Baribault et al., 2012).These results indicate the importance of identifying spatial and temporal patterns of P (Gill and Finzi, 2016), as lowland tropical forests are not exclusively limited by P, but also by base cations (Baribault et al., 2012). .

All macronutrients, including base cations, are essential for plant physiology and

subject to loss from ecosystems via gaseous emission and leaching (Asner et al., 2001, Wood et al., 2005, Corre et al., 2010, Wright et al., 2011). Potassium, in the form of monovalent K^+ cations, is particularly prone to leaching in humid tropics (Hedin et al., 2003). Although base cations may place additional constraints on plant growth (Likens and Bormann, 1995), only a few fertilisation experiments corroborate the role of base cations on nutrient limitation of lowland tropical forests (Wright et al., 2011, Baribault et al., 2012). In contrast to N and P, the possibility of K that may limit NPP has been almost entirely overlooked as only one fertilisation experiment includes K among numerous experiments throughout the tropics (Wright et al., 2011).

Phosphorus limitation is explored further.

2.3 Phosphorus limitation

A wide range of studies document that tree growth and NPP are mainly constrained by soil P availability in tropical forests (Vitousek and Sanford, 1986, Crews et al., 1995, Herbert and Fownes, 1995, Sollins, 1998, Tiessen, 1998, Cleveland et al., 2002). A meta-analysis reports that P availability regulates NPP in lowland tropical forests (Cleveland et al., 2011). In Amazonia, NPP strongly correlates with soil and foliar P concentrations, suggesting that tropical forests are likely to be P limited (Porder et al., 2007, Vitousek et al., 2010). Aboveground NPP strongly correlates with soil P as well as P uptake in West Kalimantan (Paoli et al., 2005). In addition, P appears the primary

driver of spatial patterns of NPP in Bornean tropical forests (Paoli and Curran, 2007). The deficiency of P induces long-term reductions of C storage capacity due to slow P supply through deposition and lack of other external sources (Herbert et al., 2003).

High P use efficiency may indicate P limitation to NPP, in other words, less P efficient forests can be found in soils rich in available P (Vitousek, 1982, Silver, 1994). In general, P resorption is also assumed to be higher in P-limited tropical soils from the leaf economic perspective (Vitousek, 1984, Aerts, 1997b, Aerts and Chapin, 1999), although such relationship may vary due to strong heterogeneity in tropical soils (Richter and Babbar, 1991), that drives a wide range of nutrient conditions, or related to longer leaf life spans of tropical plants (Aerts and Chapin, 1999). Increasing P use efficiency in low P availability is derived from increased retention time of P in biomass and decreased tissue P concentration (Dalling et al., 2016).

Such divergent growth strategies may be related to trade-offs in plant communities. Plant communities on P-rich soils favour fast growth at the cost of shorter leaf life spans and fast canopy P turnover, whereas those on P-poor soils favour lower P loss and longer leaf life spans at the cost of fast growth (Paoli et al., 2005). Species replacement along a soil gradient may occur due to trade-offs associated with nutrient use (Paoli et al., 2005). The former fast-growing species with higher short-term productivity per leaf mass tend to dominate in fertile soils, while the latter slow-growing species tend to dominate in infertile soils (Chapin, 1980, Aerts, 1995).

2.4 Is nitrogen abundant relative to phosphorus?

In general, the limitation of P availability and low total P is derived from long periods of leaching and strong adsorption or occlusion of P with iron and aluminum oxides (Baillie et al., 2006). A primary forest maintains higher soil concentration and stock of Hedley labile extractable P than secondary forests where soil P stocks decrease over time (Johnson et al., 2001). In contrast, secondary forests store considerable amount of N, less P, but more Ca in soil in Amazonia (Johnson et al., 2001, Feldpausch et al., 2004). In contrast to P, soil N concentration and stock tend to remain consistently larger than aboveground N stock through time (Johnson et al., 2001, Feldpausch et al., 2004), suggesting N is rather abundant relative to P. The signal of P being a major limiting element may be reflected in lower tissue P concentrations or in higher P resoprtion efficiency (Dalling et al., 2016). The prevalence of N_2-fixers in P-limited soils suggests that increasing N availability may indirectly influence P uptake (Dalling et al., 2016), as phosphatase production is N-intensive (Houlton et al., 2008). Trees of leguminous family are widely found throughout the tropics, which enhance N availability through their symbioses with N-fixing bacteria (Crews, 1999). This indicates that lowland tropical soils are generally N-rich but P-poor (Vitousek, 1982, Hedin et al., 2003, Hedin, 2004). Luxury N consumption leads to accumulation that N cannot be reused further by the tree (Lawrence, 2001). In addition, a shift from P towards N limitation can occur due to the greater mobility of soil N in disturbed forests (Herbert et al., 2003).

Pools of plant extractable nutrients are considerably lower than total soil pools (Brown and Lugo, 1990). The plant uptake of N and P may be largely supported via mycorrhizal associations namely vesicular-arbuscular mycorrhizae and ectomycorrhizae, which mobilise N and P from soil organic matter (Read and Perez-Moreno, 2003, Plassard and Dell, 2010) even at low soil concentrations. The latter is known to associate with Dipterocarp species, a predominant family in Borneo (Alexander, 1989, Smits, 1994, Plassard and Dell, 2010). Ectomycorrhizal fungi improve P uptake through more extensive soil exploration and enhanced access to occluded, primary mineral, and organic forms of soil P (Dighton, 1991, Fox and Comerford, 1992, Boot et al., 1994, Blum et al., 2002). While P appears to be not limited in the presence of intact mycorrhizal associations (Burslem et al., 1994), a study in West Malaysia shows vesicular-arbuscular mycorrhizal fungi are reduced by 25% following selective logging and by 75% following heavily logging (Alexander et al., 1992).

2.5 Multiple nutrient limitations

Our understanding of nutrient limitation has shifted from an early view of single-nutrient limitation derived from the historical Liebig's Law of the Minimum towards theories of co-limitation by multiple nutrients over the past two decades (Chapin et al., 1987, Gleeson and Tilman, 1992, Danger et al., 2008, Harpole et al., 2011). Interactions

between multiple limiting nutrients and their linkage with biogeochemical processes are more important than a single element limitation of N or P (Townsend et al., 2011).

Several fertilisation experiments conducted across the tropics (Cuevas and Medina, 1988, Lawrence, 2001, Vincent and Davies, 2003, Campo and Vazquez-Yanes, 2004, Davidson et al., 2004, Palmiotto et al., 2004, Cleveland and Townsend, 2006, Davies and Semui, 2006, Barron et al., 2008, Kaspari et al., 2008, Wright et al., 2011, Wright et al., 2018, Mori et al., 2020) illustrate multiple nutrient limitations to nutrient allocation, tree growth, and litter decomposition, and their interactions to species richness and soil types. However, it is poorly known which nutrient or nutrients limit NPP and C storage in most tropical forests, and to what extent nutrient availability affects ecosystem functioning (Cleveland et al., 2011, Townsend et al., 2011). Fertilisation experiments may fail to demonstrate co-limitation contexts as nutrient requirements for productivity vary depending on species or tissue types (Dalling et al., 2016). Nevertheless, most models of tropical C cycle normally encapsulate only single-element limitation, and multiple interactions among biogeochemical cycles are not included in projections of biosphere-atmosphere CO2 exchange due to an overall paucity of nutrient data as compared to non-tropical biomes (Townsend et al., 2011).

Key biological processes of nutrient cycling are reviewed as follows.

2.6 Nutrient uptake and nutrient uptake efficiency

Annual N and P uptake are generally quantified as NPP multiplied by tissue-specific N and P concentrations (Gill and Finzi, 2016).

Nutrient uptake = the estimation of NPP and nutrient stoichiometry (in this case, the ratio of each nutrient to C for the calculation)

Nutrient uptake efficiency = the proportion of available soil nutrients acquired by plant

Nutrient uptake is required to replace the inevitably lost nutrients in senesced leaves. The relative costs of acquiring nutrients via root system and resorption determines the proportion of nutrients from the two sources, soil and resorption, deployed in new leaves. A model by Wright and Westoby (2003) outlines that the balance is set where soil nutrients become less costly to obtain than those through resorption, thus setting the extent to which nutrients need to be extracted from senescing leaves. In this model, soil nutrients are costlier in infertile soils.

2.7 Nutrient use efficiency

Nutrient use efficiency is estimated as the ratio of biomass increment to nutrient requirement (Hirose, 1975), i.e. total NPP per unit of nutrient usage (Bridgham et al.,

1995) and largely reflects the mean stoichiometry of the living biomass weighted according to the productivity of each organ.

Nutrient use efficiency = total NPP per nutrient uptake

Plants on less fertile soils tend to use nutrients more efficiently as indicated by less nutrient return via litterfall to soil (Silver, 1994). Nutrient use efficiency can be measured at leaf, plant or ecosystem scale (Grubb, 1989, Ewel and Hiremath, 1998). Previous studies in tropical forests have focused either on the nutrient use efficiency of fine litter production (Silver, 1994, Kitayama et al., 2000) or photosynthetic leaves (Hidaka and Kitayama, 2013), but comprehensive studies of whole-forest nutrient use efficiency are scarce (e.g., Hiremath et al., 2002, Paoli et al., 2005). Nutrient use efficiency is also a key concept for understanding how resource availability determines spatial patterns of NPP (Chapin, 1980, Vitousek, 1982). For example, high phosphorus use efficiency may indicate P limitation to N:P ratio: in other words, less P efficient forests can be expected to be found on P-rich soils (Vitousek, 1982, Silver, 1994).

Leaf economics perspectives that plants on nutrient-limited soil are considered to have high nutrient use efficiency as less nutrient returns to soil via litterfall (Aerts, 1997a, Aerts and Chapin, 1999). In a fertilization experiment in Hawaii, P limitation results in high P-use efficiency, suggesting that resource use efficiency increases as resource supply becomes scarce (Harrington et al., 2001).

A recent global meta-analysis shows that P-use efficiency is highest in lowland tropical forests, where N:P ratio is highest, suggesting that tropical plants have growth strategies to maximise productivity under P-limited conditions (Gill and Finzi, 2016). A pan-tropical analysis also demonstrates that aboveground NPP per unit soil P is larger in low-P sites than high-P sites (Cleveland et al., 2011).

2.8 Nutrient resorption

Under the regime of nutrient limitation, while plants have evolved to optimise nutrient uptake and growth, resorption is a complementary strategy to meet the nutrient requirement. It is one of the key processes in biogeochemical cycling (Aerts, 1996, Jackson et al., 1997, Gordon and Jackson, 2000, Vergutz et al., 2012), in which plants withdraw mobile nutrient elements from senescing leaves before abscission. In other words, it is a functional disconnection in foliage that stays attached to the plants, which enables them to minimise the loss of growth-constraining nutrients and to be less dependent on nutrient uptake from the soil (Aerts, 1996, Eckstein et al., 1999, van Heerwaarden et al., 2003).

> Nutrient resorption = a mechanism to reduce nutrient losses by which plants withdraw mobile nutrient elements from senescing leaves before abscission

It is an important plant nutrient conservation strategy, because a major part of nutrient

capital is concentrated in plant foliage (Chapin, 1980, Eckstein et al., 1999), and it determines how much nutrients are returned to soil from plants via litterall (Vitousek, 1982, Quested et al., 2003). Resorption efficiency is estimated as the percentage difference in nutrient concentrations between green and senesced leaves, and affects key processes such as nutrient uptake, carbon cycling and tree growth (Killingbeck, 1996, Kobe et al., 2005, Berg et al., 2008).

About 50% of foliar N, P and K is assumed to be resorbed by plants (Aerts, 1996, Killingbeck, 1996, Huang et al., 2007, Yuan and Chen, 2009, Chapin et al., 2011), however this figure needs to be quantified for specific plants and vegetation types, and for other nutrient elements including base cations particularly in wet tropics where substantial leaching occurs (Cuevas and Medina, 1988, Vitousek and Howarth, 1991). High resorption efficiency is considered to be common in infertile soil (Aerts, 1996). A theoretical model suggests that along a soil fertility gradient the unit cost of nutrient resorption decrease relative to the cost of nutrient uptake from the soil (Wright and Westoby, 2003), that is, nutrient resorption is relatively more important in less fertile soils.

A meta-analysis by McGroddy et al. (2004) reports that P resorption is greater relative to N and C in tropical forests, while available data is especially limited for base cations (Aerts, 1996, Lambers et al., 1998, Kazakou et al., 2007, Yuan and Chen, 2009). Leaf mass loss should also be taken into account for the unbiased estimation as leaf mass changes during senescence (van Heerwaarden et al., 2003, Kazakou et al., 2007),

mainly due to the resorption of C and nutrients followed by leaching and *in situ* decomposition (Vergutz et al., 2012). Improved estimates of resorption efficiencies are imperative for predicting long-term NPP and nutrient cycling (Jackson et al., 1997, Gordon and Jackson, 2000, Thornton et al., 2007, Chapin et al., 2011).

Another meta-analysis documents that about half of N and P in green leaves is resorbed during senescence, and indicates that resorption efficiencies are likely to increase under lower soil availability. Similarly, the efficiency of foliar P resorption has been shown to vary with soil P availability (McGroddy et al., 2004), although the study does not incorporate the mass loss correction factor (MLCF) (Yuan and Chen, 2009).

In general, P resorption is assumed to be higher in P-limited tropical soils from the leaf economic perspective (Vitousek, 1984, Aerts, 1997b, Aerts and Chapin, 1999), although such relationship may vary due to strong heterogeneity in tropical soils (Richter and Babbar, 1991), that drives a wide range of nutrient conditions, or related to longer leaf life spans of tropical plants (Aerts and Chapin, 1999).

In addition to foliar resorption, wood resorption may exist during the transition of sapwood to heartwood. This is indicated by a meta-analysis suggesting that heartwood nutrient concentrations are substantially lower that sapwood concentrations (Meerts, 2002). In Panama, wood P is also lower in the inner annulus than the outer annulus (Heineman et al., 2016). As the focus of Meerts (2002) is

primarily temperate species, more explicit analyses of sapwood and heartwood in tropical species are necessary to address the potential wood resorption.

The impact of logging disturbance on nutrient cycling is reviewed as follows.

2.9 Logging effect on nutrient cycling

A gradient of logging disturbance also helps to understand the situation of tropical regrowth forests, which represents ~30% of the total tropical forest area (Pan et al., 2011). Previous nutrient studies have been exercised mostly in undisturbed forest ecosystems. Only 30% of the existing tropical forest area is relatively undisturbed or intact (Potapov et al., 2008), whereas the remaining area has been disturbed mostly through selective logging, which underlines the necessity of understanding nutrient dynamics in secondary growth forests (McGrath et al., 2001, Gomes and Luizao, 2012). While the majority of studies in disturbed and secondary forests have focused on Amazonia (Johnson et al., 2001, Feldpausch et al., 2004, Markewitz et al., 2004, Davidson et al., 2007, Gomes and Luizao, 2012), little emphasis has been put in Southeast Asia. Malaysian Borneo (states of Sabah and Sarawak) is one of the global hotspots of such disturbance such as deforestation and forest degradation (Fisher et al., 2011). By 2009, 28% of the original forest area had been converted to plantations, predominantly oil palm, 72% of the remaining forest area had been selectively logged (Bryan et al., 2013).

Disturbance creates canopy openings and disrupts soils, resulting in the high densities of pioneer species in secondary forests (Brown and Lugo, 1990). Higher proportions of light-demanding taxa are associated with areas of highly disturbed forests (Fairhead and Leach, 1998, ter Steege and Hammond, 2001), because logging alters the light environment (Whitmore, 1984). In addition, such pioneer species are generally characterised by high growth and mortality rates, short leaf life spans, high tissue N and P concentrations, and low wood density (Swaine and Whitmore, 1988, Raaimakers et al., 1995, Reich et al., 1995). These traits may enable pioneer species to colonise open microsites of high-light availability (Davies, 1998).

Logging changes forest structure, species composition and microclimate, and consequently alters nutrient uptake. Nutrients are removed as timber, and logging operations and the release of a large quantity of nutrients from necromass lead to the erosion and leaching of soil nutrients (Steege et al., 1996). The effect of logging on nutrient budgets is related to logging intensity, logging period, tree species, rainfall pattern, and soil properties (Kobayashi, 1994). In Malaysian Borneo, Imai et al. (2012a) documented that exported amounts of C, N and P increased linearly with increasing logging intensity, and heavy selective logging would induce P-limitation in the following regrowth period. Remote sensing analysis by Asner and Vitousek (2005) indicated that a nitrogen-fixing tree doubled N concentration in canopy, which replaced native species in disturbed forests. Calcium deficiency is also documented after logging in Sabah (Nykvist, 1997, Nykvist, 1998, Nykvist, 2000). In contrast, the study

in the Brazilian Atlantic forest demonstrated that selective logging had no effect on nutrient concentrations and C:N ratio in the soil or in the litter, although leaf litter production and input decreased (Villela et al., 2006). In the eastern Amazon, deforestation caused a temporary shift from P limitation in old-growth forests, to N limitation in converted pastures and early successional forests, and to increasing P constraints when forests become mature again (Davidson et al., 2007). This can be explained by the fact that forest conversion induces greater N losses relative to those of P, and then N fixation restores N stocks over long-term (Townsend et al., 2011). The recent study by imaging spectroscopy suggests that phosphorus limitation is intensified as logged forests recover in Malaysian Borneo (Swinfield et al., 2020).

These inconsistent findings across the tropics underscores the need of understanding the impacts of logging intensity on nutrient dynamics in particular disturbed forests in comparison with undisturbed forests.

2.10 In the context of Malaysian Borneo

Approximately 53% of Borneo remains forested, of which 54% was intact in 2010 (Gaveau et al., 2014). Between 1973 and 2010, a 30% forest loss was recorded. The proportion of intact forest is lower in Malaysian Borneo (19% in Sabah and 15% in Sarawak) than in Brunei and Kalimantan. About 10% of Borneo is converted to oil palm (*Elaeis guineensis*), or acacia (*Acacia* spp) and rubber tree (*Hevea brasiliensis*)

plantations (Casson, 2000, Carlson et al., 2012, Gaveau et al., 2014).

Selective logging, in which only a few stems per hectare are removed, is widely practiced in the tropics including Bornean tropical forests (Meijaard and Sheil, 2007a, Edwards and Laurance, 2013). In Malaysia, the majority of commercially valuable Dipterocarp species (>60 cm diameter at breast height [DBH]) and non-Dipterocarp species (>45 cm DBH in the state of Sarawak) are primarily harvested during an initial selective logging (Pinard and Putz, 1996, Kammesheidt et al., 2003, Sist et al., 2003). The following harvest takes place 25-30 years later, although this period appears insufficient to allow full recovery of timber stocks (Pinard and Putz, 1996, Sist et al., 2003, Putz et al., 2008). Despite their lower biomass and altered tree stand structure and composition, logged forests may harbour a considerable proportion of the forest biodiversity (Edwards et al., 2011), and may provide buffer zones and biological corridors in plantations (Meijaard and Sheil, 2007b). However, despite having high conservation value compared to plantations, logged forests are vulnerable to conversion to oil palm or timber plantations (Edwards et al., 2011).

2.11 Nutrient stocks in logged forests over time

A net increase of total system nutrient stocks (in soil and vegetation), particularly for N and Ca, is documented over time following disturbance, presumably due to atmospheric deposition, N_2 fixation, and subsoil uptake of leached nitrate (Szott et al.,

1991), while P remains constant, indicating a potential limitation in system productivity. Both foliar and wood P, and soil extractable P concentrations decline as secondary forests age (Feldpausch et al., 2004). Soil P stocks remain low even following fertilization in the Neotropics (Feldpausch et al., 2004). Ecosystem losses of P are of great concern due to small atmospheric inputs of P, and soil adsorption that effectively withdraws P from the biogeochemical cycle (Markewitz et al., 2004). There is also relocation of P and accrual of base cations from available soil to plant uptake as secondary forests mature, as colonising plants acquire more soil P and cations than are available (Johnson et al., 2001, Feldpausch et al., 2004), probably via subsoil uptake (Szott et al., 1999). This suggests that further removal of trees could impede forest regeneration in consequence of nutrient limitations (Johnson et al., 2001, Feldpausch et al., 2004).

How nutrient stocks in logged forests change over time in succession is yet uncertain. Aggrading forests greatly demand essential plant nutrients (Davidson et al., 2007). As a result of high nutrient concentrations in pioneer species and a relatively larger proportion of total aboveground biomass in nutrient-rich foliage, nutrient stocks in young successional forests may reach the magnitude of those in mature forest faster than C stocks (Vitousek and Reiners, 1975). In contrast, wood accumulates nutrient capital slower than foliage (Johnson et al., 2001). Nutrient cycling appears to recuperate in chronosequence studies in Amazonia (Markewitz et al., 2004, Davidson et al., 2007). Secondary forest regrowth restores aboveground nutrients loss following disturbance, with the large nutrient accrual in wood as the forests age (Markewitz et

al., 2004), particularly for Ca followed by N. In addition, N concentration and stock in soil below 30 cm depth increases with time (Feldpausch et al., 2004), although this appears to be largely contributed by N_2 fixing plants (Szott et al., 1999). It is yet uncertain whether Dipterocarp-dominated tropical forests in Borneo follow similar patterns of forest succession in legume-rich Amazonia.

Reported limitations of cations during forest succession are mixed. In Amazonia, topsoil and leaf Ca and Mg concentrations are known to decline with forest age in secondary forests (Johnson et al., 2001, Gomes and Luizao, 2012), while foliar and wood cations (K, Ca and Mg) concentrations show no trends with forest age in another study (Feldpausch et al., 2004). Soil Ca initially increases following cutting and burning, but colonising trees act as sinks and eventually reduces soil Ca (Feldpausch et al., 2004).

In contrast, selective logging may increase soil availability of base cations over long periods of time due to increased mineralization and decreased plant uptake (McNabb et al., 1997). Atmospheric deposition may also replenish depleted soil and nutrient stocks (Vitousek and Sanford, 1986, Schroth et al., 2001).

2.12 Interspecific variation

A wide range of tree functional traits (e.g. N-fixation, shade-tolerance or light-demand,

root length) related to nutrient uptake and use are likely to constrain nutrient cycling. For example, interspecific variations in foliar nutrient concentrations control plant-soil microbial feedbacks (Vitousek, 2004, Wood et al., 2011), which constrain nutrient availability through nutrient deposition and mineralisation from plant materials (Wardle et al., 2004). Species associated with high soil availability generally contain higher N and P concentrations in green leaves than species associated with low soil availability (Tanner, 1977, Andersen et al., 2012, Katabuchi et al., 2012, Dalling et al., 2016).

Spatial heterogeneity of soil nutrient availability can constrain distributions of tropical tree species at local and regional scales (John et al., 2007, Baldeck et al., 2013, Condit et al., 2013). Plants adapt to local nutrient availability through changes in species composition and adaptation. In Amazonia, species characterised with high wood density and low foliar nutrient concentrations occur on infertile soils, while species with opposite characteristics grow in fertile soils (Fyllas et al., 2009, Patiño et al., 2009). Limitation of multiple nutrients may results from variation in nutrient requirements among taxonomic and functional groups (Baribault et al., 2012).

Improving estimates of ecosystem processes in diverse tropical forests requires species-specific nutrient data (Cornwell et al., 2008).

2.13 Nutrient allocation to woody components (Chapter 4)

Wood is considered to contain roughly half of macronutrients in tropical forest vegetation (Tanner, 1985, Wang et al., 1991, Stanley and Montagnini, 1999, Bond, 2010). However, while foliar nutrient concentrations are widely measured, wood nutrient concentrations are poorly quantified (Heineman et al., 2016). Along with the well-known 'leaf economics spectrum' that assembles leaf chemistry datasets (Wright et al., 2004), Chave et al. (2009) collate data of the major wood functional traits and suggest the 'wood economics spectrum'. Chave et al. emphasise that wood chemical traits, namely N, P, K, Ca and Mg concentrations in woody tissue are among the most poorly documented in the literature. In contrast to the low nutrient content of tropical soils, nutrients are accumulated in biomass, mostly in bark and foliage (Stark, 1971, Ruddle et al., 1981).

Unlike C and N which have been quantified elsewhere (Kauffman et al., 1995, Liu et al., 2003, Harmon et al., 2004, Becker et al., 2012, Martin et al., 2014, Nakagawa et al., 2016), direct measurements of P (probably the most important limiting element for tropical forests) concentrations and stocks in wood (Johnson et al., 2001, Feldpausch et al., 2004, Heineman et al., 2016) and fine roots (Li et al., 2010) are scarce in the tropics, particularly in Southeast Asia (e.g., Aoyagi and Kitayama, 2016). By contrast, soil and leaf P concentrations are widely documented (Crews et al., 1995, Coomes, 1997, Wright et al., 2004, Wright et al., 2005, Hidaka and Kitayama, 2009). While N-rich enzymes regulate photosynthetic CO_2 fixation (Field and Mooney, 1986, Reich et

al., 1997), P-rich RNA and ATP determine cellular biosynthesis (Sterner and Elser, 2003). In addition, cations such as K, Ca and Mg are required for tree metabolism and physiological processes related to growth as well as wood formation (Fromm, 2010). The prediction of wood nutrient contents from leaf contents is necessary to improve models predicting carbon turnover from woody biomass (Cornwell et al., 2009).

Nutrient allocation is constrained between leaf and wood at the species level, supporting results of previous meta analyses which show that N and P allocation is constrained across plant organs (Kerkhoff et al., 2006, Ågren, 2008).

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Chapter 3 Site description and methods

This chapter describes the study sites across two states of Malaysian Borneo, Sabah and Sarawak, and defines a logging disturbance gradient comprising nine plots used in the study. In addition, field sampling and laboratory methods are described in detail.

Seven study plots are located in the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, and two plots are located in Lambir Hills National Park in Sarawak. These plots are part of the Global Ecosystem Monitoring (GEM) network (Marthews et al., 2014, Malhi et al., 2021), see http://gem.tropicalforests.ox.ac.uk/ for more details..

3.1 Site description

SAFE Project

The SAFE Project (http://www.SAFEproject.net) is one of the world's largest ecological experiments in the Malaysian state of Sabah, designed as a landscape-scale fragmentation study with 42 experimental fragments of 1, 10 to 100 ha. SAFE Project examines impacts of logging and forest conversion to oil palm plantation on biodiversity, ecosystem functioning and productivity, and expands on previous visionary experiments such as the Biological Dynamics of Forest Fragments Project in Brazilian Amazon. The experimental area is 7,200 ha of lowland Dipterocarp rainforest within the Kalabakan Forest Reserve (4°43′ N, 117°35′E), the majority of which is subject to conversion to oil palm plantation. The SAFE Project was launched

in 2011, providing an opportunity to collect pre-fragmentation data (Ewers et al., 2011).

While comparative analyses between unlogged and logged forests are common for logging-impact studies, which may not fully explain spatial heterogeneity in disturbance and inherent environmental gradients, the SAFE Project provides a disturbance gradient ranging from old-growth to forest logged multiple times (Struebig et al., 2013). One novel aspect of the SAFE Project is to examine the impacts of repeated logging (between two and four rounds of logging since the 1970's across the area) prior to conversion to oil palm plantation rather than the effects of a single rotation of logging. Such a modification process is similar to the real-world pattern of forest modification across the tropics today, ensuring that the outputs of the SAFE Project should be directly relevant to policy decisions about land-use change (Ewers et al., 2011).

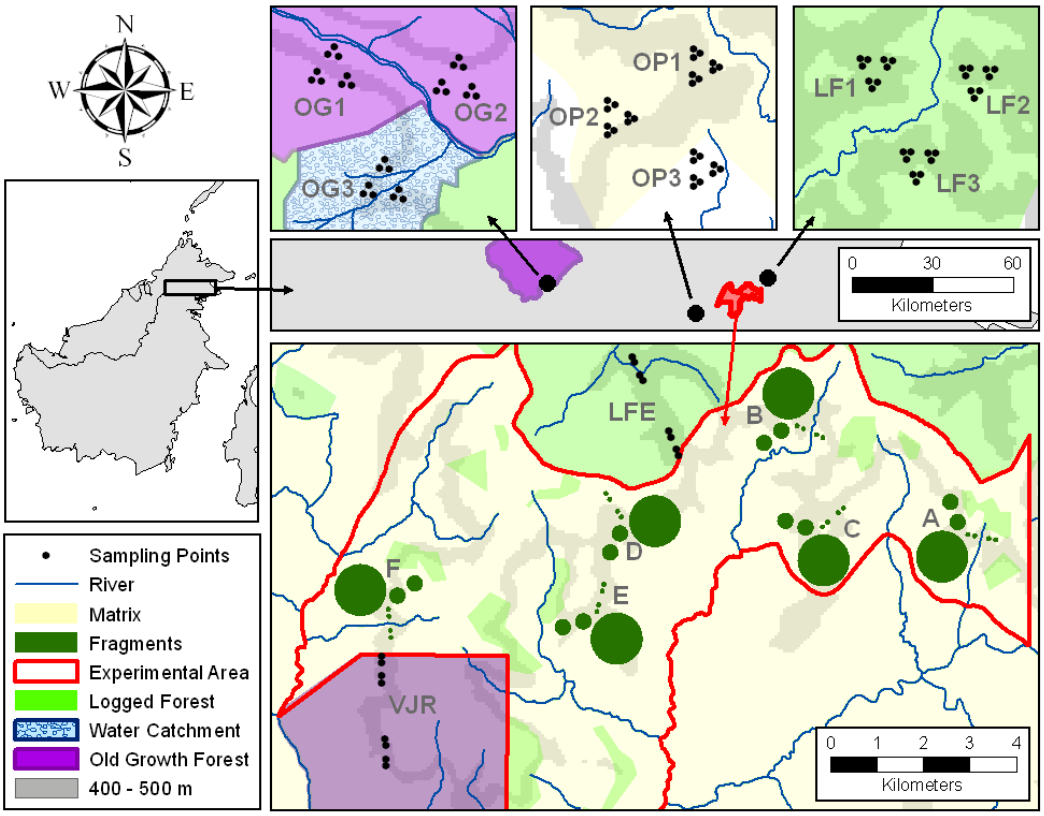


Figure 3.1 Map of the Stability of Altered Forest Ecosystems (SAFE) Project in the Malaysian state of Sabah

(derived from http://www.SAFEproject.net). The Experimental Area has been subjected to repeated logging prior to the upcoming conversion to oil palm plantation, but 800 ha of circular forest fragments comprising six blocks (A–F), are to be maintained as forest fragments within the future plantation. The Logged Forest (LF) area which has been logged twice will remain as continuous forest. Old-growth forest includes a Virgin Jungle Reserve (VJR), which will become isolated during the forest conversion, as well as OG area within the Maliau Basin Conservation Area, approximately 65 km away, which will remain as a large intact protected forest area.

For this study, I collected data in intensive carbon plots which form a gradient of logging disturbance. The plots were located within future forest fragments of B, E, continuous logged forest LF2, protected intact forest of OG1 and OG2 area and future

oil palm area near the SAFE flux tower (located between fragments B and D in Fig. 3.1). Plots are situated at approximately equal altitude and designed to reduce potentially confounding factors such as slope, latitude, longitude and distance to forest edges in advance of controlled forest conversion to oil palm (Ewers et al., 2011). The climate is aseasonal, with mean annual temperature of 27.8 °C and annual precipitation of 2,890 mm (Luasong Forestry Centre, unpublished data). Soils are acrisols and luvisols, developed over the underlying bedrock of predominantly mudstone and sandstone (Acres, 1975).

In the SAFE Project, logged forest plots vary in their logging intensity. The B and E areas had been heavily logged multiple times under four logging rotations: an estimated 113 m^3 ha^{-1} extraction during the first round in 1970's (Fisher et al., 2011), followed by the removal of further 66 m^3 ha^{-1} by re-logging three times (D. P. Edwards, unpublished data). Under a modified uniform system (Whitmore, 1984), all commercially valuable trees (> 60 cm diameter at breast height [DBH]) were extracted using tractor and high-lead cable extraction techniques during the first rotation, but the tree diameter threshold was lowered to ≥ 40 cm DBH for commercial species and ≥ 25 cm DBH for pioneer species in some areas during the subsequent rotations (Edwards et al., 2011). These heavily-logged plots are dominated by pioneer and invasive species such as *Macaranga* with few commercially valuable species remaining. There is, however, considerable heterogeneity within the logged landscape, with pockets of less heavily disturbed sites remaining. The LF plot is located within the contiguous Ulu Segama Forest Reserve, which had been logged twice: similar

extraction rate to the B and E in the first rotation, followed by 37 m^3 ha^{-1} on average in the second rotation. Dominant tree species in old-growth plots include highly-marketable species *Eusideroxylon zwageri* as well as Dipterocarp: *Shorea spp.* (Struebig et al., 2013).

All plots had a planimetric area of 1 ha, which was divided into 25 subplots of 20 m × 20 m. These plots were established to quantify the change in carbon stocks and dynamics following forest clearance and fragmentation along a gradient of logging intensity disturbance. Considering the disturbance history, we define a disturbance gradient by ranking from most to the least intensively logged based on basal area of trees (> 10 cm DBH), mean canopy gap fraction, and mean forest quality score. For mean forest quality score, individual 20 m × 20 m subplots within each 1 ha plot (*n* = 25) were subjectively ranked into the forest quality classes *a priori,* from 1 (heavily disturbed) to 5 (no signs of human disturbance), using the presence of stumps and felled trees, evidence of logging trails, number of large (≥ 30 cm DBH) trees and canopy closure as the assessment criteria (Riutta et al., 2018).

These plots are also categorised into three forest types based on the above criteria: heavily-logged (B North: SAF-02, B South: SAF-01, and Tower: SAF-05), moderately-logged (E: SAF-03, and LF: SAF-04) and old-growth (OG1: MLA-02 and OG2: MLA-01) (Table 3.1).

Lambir Hills National Park

In addition to seven plots in the SAFE Project, two 1 ha old-growth forest plots (100 × 100 m) are located within the Lambir Hills National Park in the Malaysian state of Sarawak (4°12′ N, 114°2′E), one each on clay and sandy soils (Kho et al., 2013). These plots are part of the Center for Tropical Forest Science (CTFS) 52 ha forest dynamics plot. Lambir is a hyperdiverse mixed Dipterocarp forest with 1,173 trees species identified in the 52 ha plot (Lee et al., 2002). The Lambir soils vary in depth, sand content, water-holding capacity and nutrient concentrations, particularly phosphorus (P) and magnesium (Mg) (Baillie et al., 1987, Ashton and Hall, 1992, Hirai et al., 1997, Potts et al., 2002), resulting in variation in forest floristics, structure and dynamics on the plot (Yamakura et al., 1996, Itoh et al., 1997, Palmiotto et al., 2004, Itoh et al., 2003, Potts et al., 2004, Davies et al., 2005, Russo et al., 2005). The shale-derived clay soils (LAM-07), occurring in low-lying gullies, are udult Ultisols with higher nutrient concentrations, water-holding capacity with a thin litter layer on the soil surface. In contrast, the sandstone-derived soils (LAM-06), occurring on slopes and ridges, are humult Ultisols with lower nutrient concentrations, leached, drought-prone with densely rooted raw humus on the surface horizon (Palmiotto et al., 2004, Davies et al., 1998) (Table 3.1).

3.2 Methods

Tree components were sampled in the SAFE Project during January to March in 2014, ~7–13 years after the latest round of logging ended, as well as in Lambir Hills National

Park.

Sampling of tree components for ecosystem nutrient cycling studies (Chapters 5 and 6):

Nutrient samples were collected between January and March in 2014. We selected 15 trees (≥ 10 cm diameter at breast height [DBH]), consisting of five tree species with three replicates each (*n* = 15) outside, but within 100 m of the plot boundary of each plot, representing the most common species of the plot (Table 3.3), i.e., different species were sampled adjacent to each plot, resulting in a total sample of 34 species. Sampled trees had no visible damage (e.g. no insect damage, chlorotic leaves, bent stems). Four tree components were collected from each tree: branches, green leaves, senesced leaves and fine roots. The total number of samples was 540 (5 trees species × 3 replicates × 4 components × 9 plots). Species identification was verified from collected voucher specimens of chosen trees at the herbarium of the Forest Research Centre in Sabah, Malaysia.

Mature branches with fully expanded green leaves were obtained using a long pole with a saw blade, by tugging a rope cast over a branch with a fishing rod, or by climbing. Although the collection of sun leaves is often recommended by functional trait protocols for foliar nutrient analysis (Cornelissen et al., 2003), we collected shade leaves because the majority of trees and leaves (≥ 10 cm DBH) were shaded, particularly in old-growth plots. It was also to ensure a consistency in the leaf sampling

across plots, and to match green leaves against freshly fallen senesced leaves for leaf resorption estimation assuming that the majority of fallen leaves were shade leaves. The selection of sun and shade leaves is unlikely to be influential. A study of 32 leaf traits across 284 species in Borneo, where the data were collected partly from the same plots as this study, found no systematic differences between sun and shade leaves (Both et al., 2019). Similarly, an analysis of leaf plasticity to light showed that the species ranking in mean concentrations of N and P was maintained across sun and shade leaves 38 tropical tree species in Bolivia (Rozendaal et al., 2006). All sampled branches were ≥ 1 cm in diameter and were dissected into disks. The disks were taken in the midpoint of the branch (i.e. not near the trunk nor the tip of the branch). Newly shed senesced leaves were collected from the ground; all such collected leaves were intact, fully brown and identical in shape and size to the green leaves. Twenty green and senesced leaves from each individual tree were collected for chemical analysis, and were pooled, resulting in one sample of green leaves, and one sample of senesced leaves per tree.



Figure 3.2 Typical leaf, woody and fine root samples collected in the SAFE Project (left) and Lambir Hills National Park (right)

Mature living fine roots (here defined as roots of ≤ 5mm in diameter) were excavated near to the coarse root of each sampled tree. They were sieved and washed with tap water. These samples contained not only fine roots of the target tree but also possibly of other plants as they were not able to be distinguished empirically. We, therefore, treated them as plot-level (i.e. plant community level) samples, not as individual tree samples in our study. Fine roots were, therefore, analysed for two replicates per species per plot only (*n* = 10 per plot).



Figure 3.3 Field work in the SAFE Project (left) Lambir Hills National Park, Sarawak (right)

Sampling of tree components for wood nutrient distribution study (Chapter 4):

Tree components were sampled in August 2014. Thirty trees ≥ 10 cm diameter at breast height (DBH), which consisted of 10 tree species with three replicates were selected in the study site (Table 3.2). Within each tree, 14 different locations were sampled (Fig. 4.1 and 4.2). This destructive sampling was carried out in a nearby logging site where direct felling was being conducted within the Benta Wawasan (concession holders) area. Collected voucher specimens of the trees were verified at the herbarium of the Forest Research Centre, Sabah Forestry Department in Sepilok, Sabah.

Selection of tree species:

To characterise the species composition in the study area, tree censuses were conducted during 2011 and 2012, and 1,580 trees (≥ 10 cm DBH) of 405 species were identified in five 1-ha logged-plots at the SAFE Project area (Riutta et al., 2018, Both et al., 2019). The species sampled for this study represented 25% of total number of individual stems (26%, 41% and 53% of the species, genus and family basal areas), including most abundant species by ranking: *Macaranga pearsonii* (17% abundance), and some of dominant species: *Parashorea malaanonan* (2% abundance) and *Neolamarckia cadamba* (1% abudance).

In the two old-growth forest plots in Maliau, the total number of stems, 882, comprised 239 species from 118 genera. In the two old-growth forest plots in Lambir, the total number of stems, 809, comprised 360 species representing 118 genera. The species sampled for this study accounted for 17% of the individual stems, on average, (16%, 37% and 65% of the species, genus and family basal areas) in the old-growth plots.

Dipterocarpaceae is the most dominant family in Borneo (Palmiotto et al., 2004), accounting for 19% of the stems in the study area, and a half of our sampled trees belongs to this family. This family is also favoured for logging. *Macaranga pearsonii*, *Neolamarckia cadamba* and *Trema orientalis* are considered as pioneer species (Davies and Semui, 2006, Saner et al., 2012). Hence, we sampled a broad taxonomic range from light-demanding pioneer to shade-tolerant late-successional species

(Table 3.2).



Figure 3.4 Typical wood sample collected in the field

Chemical analyses of plant tissues (Chapters 4, 5 and 6):

Concentrations of five macronutrient elements (N, P, K, Ca and Mg) and carbon (C) in each individual component were quantified at the chemistry laboratory in Forest Research Centre, in Sabah, Malaysia. First, all samples were oven dried at 50°C to constant weight for five days, and were then ground with a Thomas Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 100-mesh (212-μm) sieve. Branch samples including the bark were chipped to small pieces before grinding. Both green and senesced leaves included petioles.

Most of the protocols are described in Majalap and Chu (1992). Summary of the methods used are as follows. Each sample was digested following the sulphuric acid-hydrogen peroxide-lithium sulphate digest procedure for vegetation described in Allen (1989). Phosphorus in the digest was determined using the molybdenum-blue method described in Anderson and Ingram (1993) and read at 880 nm on a spectrophotometer (HITACHI UV-VIS, Tokyo, Japan), while K, Ca and Mg contents were measured on an atomic absorption spectrophotometer (GBC Scientific Equipment, Victoria, Australia).

Total C and N contents (as total element contents) were determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany).



Figure 3.5 Laboratory analysis at the Forest Research Centre, Sabah Forestry Department, the Head of Chemistry, Dr Noreen Majalap, in front.

Quantification of ecosystem nutrient cycles (Chapters 5 and 6):

In Chapters 5 and 6, the measurements of the nutrient content of different tree organs were combined with previously collected data See (Kho et al., 2013, Riutta et al., 2018) on net primary productivity (NPP). This study employed a novel approach of combining data of the NPP, that is, the production of new tissue (expressed in unit carbon) with data on nutrient stoichiometry, which enabled the quantification of nutrient requirement and its allocation across tree organs, for each nutrient.

The following NPP components were quantified: canopy (leaves, twigs, reproductive parts), woody (stem, coarse roots and branch), and fine roots. The data was collected using standardized GEM protocols (Marthews et al., 2014, Malhi et al., 2021). Canopy

NPP was estimated using litter traps, woody NPP of stems and coarse roots were estimated from repeated tree censuses, with biomass equations based on allometry with diameter and height, branch NPP was estimated using branch fall quadrats or transects, and fine root NPP was estimated using ingrowth cores. The NPP measurements are described in detail in Riutta et al. (2018) for the Sabah plots and Kho et al. (2013) for the Sarawak plots.

Table 3.1 Characteristics of the study plots. See Fig. 3.1 for the map.

Plot code[a]	**Plot location**	**Disturbance**	**Soil type; topography**	**Basal area of trees > 10 cm DBH (m^2 ha^{-1})**[b]	**Mean canopy gap fraction (%)**[b]	**Mean forest quality score**[c]
SAF-01	SAFE Project Experimental Area (4.732°, 117.619°), Sabah B area	Heavily logged	Clay; mostly flat with a moderate slope on one edge	6.81 ± 1.00	15.0 ± 2.14	2.2
SAF-02	SAFE Project Experimental Area (4.739°, 117.617°), Sabah B area	Heavily logged	Clay; undulating	11.1 ± 1.81	13.4 ± 1.51	2.6
SAF-05	SAFE Project Experimental Area (4.716°, 117.609°), Sabah Future oil palm	Heavily / moderately logged	Clay; undulating	13.9 ± 1.70	12.2 ± 2.07	2.7
SAF-04	SAFE Project Logged Forest Area	Moderately logged	Mostly sandy loam, partly clay; flat	19.3 ± 1.70	12.8 ± 1.03	3.2

	(4.765°, 117.700°), Sabah LF2 area					
SAF-03	SAFE Project Experimental Area (4.691°, 117.588°), Sabah E area	Moderately logged	Clay; steep slope	19.6 ± 1.88	11.2 ± 1.29	3.2
MLA-02	Maliau Basin Conservation Area (4.754°, 116.950°), Sabah OG1 area	Old-growth	Clay; moderate slope	34.7 ± 2.74	7.04 ± 0.55	5.0
MLA-01	Maliau Basin Conservation Area (4.747°, 117.700°), Sabah OG2 area	Old-growth	Clay; undulating	41.6 ± 3.59	8.70 ± 0.62	5.0
LAM-	Lambir Hills National Park	Old-growth	Clay; undulating valley	31.8 ± 3.85	10.5 ± 0.45	5.0

07	(4°12'N, 114°2'E), Sarawak		bottom			
LAM-06	Lambir Hills National Park (4°12'N, 114°2'E), Sarawak	Old-growth	Sandy loam; undulating ridge top	41.1 ± 2.45	9.52 ± 0.22	5.0

[a]Plot code as in the ForestPlots database (ForestPlots.net)

[b]DBH – Diameter at breast height (1.3 m); Basal area and gap fraction denote the mean ± 1 SE of individual subplots.

[c]Individual 20 m × 20 m subplots within each 1 ha plot (*n* = 25) were subjectively ranked into the forest quality classes *a priori,* from 1 (heavily disturbed) to 5 (no signs of human disturbance), using the presence of stumps and felled trees, evidence of logging trails, number of large (≥ 30 cm DBH) trees and canopy closure as the assessment criteria.

Table 3.2 The list of sampled tree species for the ecosystem nutrient cycling studies, grouped by successional types (n = 30; 10 species with three replicates)

Family	**Genus**	**Species**	**Height range (m)**	**DBH[a] range (cm)**	**Species code**
Dipterocarps					
Dipterocarpaceae	*Parashorea*	*P. malaanonan*	14.0 – 28.7	12.2 – 44.1	**DP.m**

Dipterocarpaceae	*Shorea*	*S. johorensis*	14.7 – 23.4	13.9 – 41.8	**DS.j**
Dipterocarpaceae	*Shorea*	*S. leprosula*	16.5 – 19.4	24.1 – 27.2	**DS.l**
Dipterocarpaceae	*Shorea*	*S. micans*	11.3 – 15.4	11.8 – 13.2	**DS.m**
Dipterocarpaceae	*Shorea*	*S. parvifolia*	12.4 – 16.5	11.7 – 20.1	**DS.p**
Other non-pioneers					
Fagaceae	*Lithocarpus*	*L. leptogyne*	9.7 – 20.6	17.2 – 24.8	**FL.l**
Malvaceae	*Pentace*	*P. laxiflora*	12.0 – 18.6	12.5 – 25.2	**MP.l**
Pioneers					
Cannabaceae	*Trema*	*T. orientalis*	13.8 – 17.7	30.2 – 33.3	**CT.o**
Euphorbiaceae	*Macaranga*	*M. pearsonii*	12.8 – 19.3	23.4 – 26.4	**EM.p**
Rubiaceae	*Neolamarckia*	*N. cadamba*	7.2 – 14.2	22.5 – 30.8	**RN.c**

Successional types were classified according to Köhler et al. (2000), Davies and Semui (2006) and Saner et al. (2012).

[a]Diameter at breast height (1.30 m).

Table 3.3 The list of 34 sampled tree species (n = 133) for the wood nutrient distribution study. Species were classified into successional types of non-pioneer species (Dipterocarps and other non-pioneers) and pioneer species[a].

Family	Genus	Species	Sample (*n* =)	DBH[b] range (cm)	Species code	Successional type	Disturbance group
				Secondary forests: Highly-logged (Hlog) and Moderately-logged (Mlog)			
Dipterocarpaceae	*Shorea*	*fallax*	3	12.1 – 19.2	DS.f	Dipterocarp	Mlog: SAF-04
Dipterocarpaceae	*Shorea*	*macrophylla*	3	13.0 – 20.8	DS.m	Dipterocarp	Mlog: SAF-04
Euphorbiaceae	*Macaranga*	*gigantea*	3	12.2 – 22.7	EM.g	Pioneer	Hlog: SAF-01
			3	12.7 – 21.4	EM.g	Pioneer	Mlog: SAF-03
Euphorbiaceae	*Macaranga*	*hypoleuca*	6	12.3 – 16.1	EM.h	Pioneer	Hlog: SAF-01, -02
			3	11.1 – 25.6	EM.h	Pioneer	Mlog: SAF-04
Euphorbiaceae	*Macaranga*	*pearsonii*	9	10.0 – 20.3	EM.e	Pioneer	Hlog: SAF-01, -02, -05
			3	10.0 – 18.6	EM.e	Pioneer	Mlog: SAF-03

Euphorbiaceae	*Mallotus*	*paniculatus*	3	20.4 – 23.5	EM.a	Pioneer	Hlog: SAF-02
Euphorbiaceae	*Spathiostemon*	*javensis*	3	11.2 – 25.0	ES.j	Non-pioneer	Hlog: SAF-01
Fabaceae (Leguminosae)	*Fordia*	*splendidissima*	3	11.7 – 14.0	FF.s	Non-pioneer	Mlog: SAF-03
Fabaceae (Leguminosae)	*Saraca*	*declinata*	3	53.5 – 89.1	FS.d	Non-pioneer	Hlog: SAF-05
			3	18.3 – 68.9	FS.d	Non-pioneer	Mlog: SAF-04
Moraceae	*Artocarpus*	*lanceifolius*	2[c]	16.8 – 17.0	MA.l	Non-pioneer	Hlog: SAF-02
Phyllanthaceae	*Antidesma*	*thwaitesianum*	3	11.5 – 12.3	PA.t	Non-pioneer	Mlog: SAF-03
Rubiaceae	*Neolamarckia*	*cadamba*	3	22.3 – 29.3	RN.c	Pioneer	Hlog: SAF-05
Rutaceae	*Melicope*	*confusa*	3	10.4 – 12.0	RM.c	Non-pioneer	Mlog: SAF-03
Styracaceae	*Bruinsmia*	*styracoides*	3	10.4 – 37.6	SB.s	Non-pioneer	Hlog: SAF-02
			3	13.3 – 19.3	SB.s	Non-pioneer	Mlog: SAF-04
Sapindaceae	*Nephelium*	*N.ramboutan-*	3	13.1 – 25.2	SN.r	Non-pioneer	Hlog: SAF-05

		ake					
Urticaceae	*Dendrocnide*	*elliptica*	6	11.6 – 26.9	UD.e	Non-pioneer	Hlog: SAF-01, -05
				Old-growth (OG) forests			
Anacardiaceae	*Gluta*	*wallichii*	3	12.1 – 13.8	AG.w	Non-pionner	OG: LAM:06
Annonaceae	*Polyathia*	*sumatrana*	3	11.1 – 13.7	AP.s	Non-pionner	OG: MLA-01
Annonaceae	*Popowia*	*pisocarpa*	3	11.6 – 14.3	AP.p	Non-pionner	OG: LAM-07
Burseraceae	*Dacryodes*	*rostrata*	3	11.9 – 26.5	BD.r	Non-pionner	OG: LAM-06
Dipterocarpaceae	*Dryobalanops*	*aromatica*	6	12.5 – 24.8	DD.a	Dipterocarp	OG: LAM-06, -07
Dipterocarpaceae	*Shorea*	*laxa*	3	10.5 – 26.0	DS.l	Dipterocarp	OG: LAM-06
Dipterocarpaceae	*Shorea*	*macroptera*	3	13.2 – 20.3	DS.m	Dipterocarp	OG: MLA-07
Dipterocarpaceae	*Shorea*	*parvifolia*	3	13.5 – 18.8	DS.p	Dipterocarp	OG: MLA-01
Euphorbiaceae	*Elateriospermum*	*tapos*	3	22.5 – 29.1	EE.t	Non-pionner	OG: LAM-06
Euphorbiaceae	*Koilodepas*	*longifolium*	3	10.6 – 13.6	EK.l	Non-pionner	OG: MLA-02

Euphorbiaceae	*Mallotus*	*wrayi*	3	10.1 – 11.6	EM.w	Non-pioneer	OG: MLA-01
Lauraceae	*Eusideroxylon*	*zwageri*	6	24.8 – 95.5	LE.z	Non-pionner	OG: MLA-01, -02
Myristicaceae	*Knema*	*laurina*	3	10.8 – 20.6	MK.l	Non-pionner	OG: MLA-02
Phyllanthaceae	*Cleistanthus*	*megacarpus*	2[c]	10.0 – 14.2	PC.m	Non-pionner	OG: MLA-01
Sapotaceae	*Palaquium*	*calophyllum*	3	11.9 – 26.5	SP.c	Non-pionner	OG: LAM-07
Simaroubaceae	*Allantospermum*	*borneense*	3	17.5 – 51.6	SA.b	Non-pionner	OG: LAM-07
Symplocaceae	*Symplocos*	*fasciculata*	3	21.5 – 23.9	SS.f	Pioneer	OG: MLA-02
Tetramelaceae	*Octomeles*	*sumatrana*	3	19.4 – 20.8	TO.s	Pioneer	OG: MLA-02

[a]Successional types were classified according to Köhler et al. (2000), Davies and Semui (2006) and Saner et al. (2012).

[b]Diameter at breast height.

[c]One of supposed *Artocarpus laceifolius* and *Cleistanthus megacarpus* samples was wrongly identified; therefore these species represent only two samples (*n* = 2).

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Chapter 4, Overview

In this chapter, I examine how the concentration of six key elements (carbon, nitrogen, phosphorus, potassium, calcium and magnesium) and wood density vary in the wood of ten South East Asian tree species, both radially and along the length of the tree. The radial analysis includes bark, sapwood and heartwood, and the vertical analysis include coarse roots, bottom of the trunk, middle of the trunk, bottom of the branch, middle of the branch and top of the branch. Furthermore, I quantify wood resorption rates by comparing sapwood and heartwood nutrient concentrations.

This chapter is, to my best knowledge, the first quantification of macronutrient distribution across woody components for tropical trees which considers both vertical and radial variation, and the first estimates for all five macronutrients in coarse roots in tropical forests.

I designed the experiment together with my supervisors and collected all the data. I led on data processing, analysis and writing. Noreen Majalap-Lee led the chemical analyses of the samples and helped with the logistics of the fieldwork. Reuben Nilus helped with the logistics of the fieldwork and species identification and commented on the manuscript. James Josue helped with the laboratory analyses and wood density samples.

Chapter 4 Radial and vertical variation of wood nutrients and wood density in Bornean tropical forest trees

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Abstract

Nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) concentrations in woody tissue are poorly documented, but are necessary for understanding whole-tree nutrient use and storage. Here we report how wood macronutrient concentrations vary radially and along the length of a tree for 10 tropical tree species in Sabah, Malaysia. To our knowledge, this is the first detailed quantification of nutrient allocation across woody components in tropical forests, considering vertical and radial variation within a whole tree.

Bark nutrient concentrations were consistently high: 2.9-13.7 times greater than heartwood depending on the nutrient. In contrast, within the wood both the radial (sapwood vs heartwood) and vertical (trunk bottom and middle) variation was modest.

Higher concentrations in sapwood relative to heartwood provide empirical support for wood resorption during sapwood senescence. Dipterocarp species showed resorption rates of 25.3±7.1% (N), 62.7±11.9% (P), and 56.2±12.5% (K) respectively, while non-dipterocarp species showed no evidence of nutrient resorption in wood. This suggests an efficient nutrient conservation mechanism specific to this family and that the lower wood nutrient concentrations in dipterocarps are largely compensated by wood resorption. In contrast, Ca and Mg tended to accumulate in heartwood, suggesting either that heartwood is a repository for these nutrients, or that they play a functional role, for example in providing strength. Wood density showed little vertical variation along the trunk.

As our study showed exceptionally high nutrient concentrations in the bark, debarking during logging operations could substantially contribute to maintaining nutrients within forest ecosystems.

Key words: bark, coarse roots, heartwood, Malaysian Borneo, nutrient cycling, SAFE Project, sapwood, wood traits

INTRODUCTION

Wood plays key functional roles in trees, including mechanical stability, defense against predators, pathogens and natural hazards, water and nutrient transport, as well as resource storage (Chave et al., 2009). Constituting > 90% of the plant mass, wood contains approximately half of the macronutrient elements – nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) in tropical forest vegetation (Tanner, 1985, Wang et al., 1991, Stanley and Montagnini, 1999, Bond, 2010), and stores more carbon (C) than any other plant organ: ~425 Pg of C globally (Denman et al., 2007).

While great attention has been given by ecologists to the link between interspecific variation in leaf traits and patterns of N and P cycling both within and across forest types (Chapin, 1980, Reich et al., 1992, Reich et al., 1997, Ordoñez et al., 2009), interspecific variation in wood chemical traits for nutrient dynamics has historically not been well studied (Vitousek and Sanford, 1986). Wood chemical traits have been hypothesised to covary along the 'wood economics spectrum' (WES; Chave et al., 2009) with wood density, which could represent an easily measurable proxy for life-history strategy among co-occurring tree species (Wright et al., 2003). Such covariation can be expected when considering a functional tradeoff between 'storage/defense' and 'growth' as a selective pressure that drives interspecific variation in wood chemistry (Martin et al., 2014). However, the conceptual framework of WES

acknowledges a near complete lack of information on species-specific wood chemical traits such as nutrient concentrations among trees (Chave et al., 2009, Martin et al., 2013, Martin et al., 2014). In addition to widely quantified foliar nutrient concentrations, which empirically support the conceptual framework of leaf economics spectrum (LES; Wright et al., 2004), direct measurements of wood nutrient concentrations are necessary to understand the whole-tree nutrient use of tropical tree species and its implication for ecosystem processes (Heineman et al., 2016).

There is likely to be broad variation in anatomical, chemical, physical and mechanical properties, as well as nutrient concentrations in different plant organs (Meerts, 2002, Lachenbruch et al., 2011). The study on such variation may help understand how natural selection shapes plants, particularly their xylem throughout their life-history (Lachenbruch et al., 2011). Nutrient allocation among plant organs constrains plant growth and life-history strategies (Grime, 2001, Kerkhoff et al., 2006). While wood is usually considered to have the lowest concentrations among all organs (Tsutsumi et al., 1968), wood nutrient concentrations are expected to vary substantially within a tree (Hillis, 1987) and overall wood nutrient stocks may be a substantial component of ecosystem nutrient reservoirs. Wood accumulates nutrient capital more slowly than foliage (Johnson et al., 2001), but C and nutrient stores in wood can be used to build new biomass, offsetting biomass losses due to branch falls and damages (Chapin et al., 1990, Poorter and Kitajima, 2007).

It is also necessary to consider differences in nutrient contents between heartwood

and sapwood to compute nutrient budgets and fluxes for individual trees and forest stands (Turner and Lambert, 1983, Augusto et al., 2000, Heineman et al., 2016). Sapwood and heartwood are anatomically different. Inner sapwood rings are eventually converted to heartwood (duramen), which no longer contains living cells and often has vessels blocked with tyloses and accumulates secondary compounds (Bamber and Fukazawa, 1985, Hillis, 1987). Nutrient resorption occurs during the transition of sapwood to heartwood, indicated by a meta-analysis showing that heartwood has substantially lower nutrient concentration than sapwood (Meerts, 2002). A recent study in Panama also indicates P resorption as inner annulus have lower P than outer annulus (Heineman et al., 2016). Analyses on how wood nutrient concentrations vary across woody components including branches, roots, sapwood and heartwood are especially limited in the tropics (Meerts, 2002, Nakagawa et al., 2016).

Bark is a morphologically diverse and functionally important component of the stem (Romero, 2014), and its functions include pathogen and fire protection (Paine et al., 2010, Poorter et al., 2014), corticular photosynthesis (Pfanz, 2007, Rosell et al., 2015), water and photosynthate storage, and mechanical support (Rosell and Olson, 2014). Bark plays a vital role in nutrient dynamics, maintaining higher concentrations of nutrients than other woody tissues and acting as a protein store (Wetzel and Greenwood, 1989, Jenkins et al., 2003). Bark photosynthesis contributes up to 11% of twig wood C (Cernusak and Hutley, 2011). Furthermore, bark chemistry has not been considered in comparative studies of bark traits (Rosell et al., 2014), although it

may play a role in life-history strategy among tree species (Martin et al., 2014).

Wood density (WD) is a key trait for life history variation of tree species, because it represents C allocation to stem tissue, and tends to correlate with growth and mortality (Enquist et al., 1999, Muller-Landau, 2004, van Gelder et al., 2006, Preston et al., 2006, Swenson and Enquist, 2008). Previous studies demonstrate a negative correlation between height growth and WD (Niklas, 1993, Poorter, 2008), while reported relationships between WD and total tree height are mixed (Falster and Westoby, 2005, Preston et al., 2006, Poorter, 2008, Swenson and Enquist, 2008). In addition, wood nutrients need to be quantified in combination with WD to better understand plant functional traits in tropical forests (Heineman et al., 2016). While wood density positively correlated with wood N for tree species in Panama (Martin et al., 2014), no relationship was found between WD and wood N content in Uganda (Becker et al., 2012).

The aim of this study is to examine how nutrient concentrations and WD vary within trunk cross-section and along the length of the tree in concert with WD in a Bornean tropical forest, and to assess inter- and intra-specific patterns. Previous direct measurements of macronutrients are entirely based on extracted wood cores (Johnson et al., 2001, Feldpausch et al., 2004, Heineman et al., 2016). Ours is therefore the first study of macronutrient distribution across the woody components of tropical trees, considering both vertical and radial variation. To our knowledge, these

are also the first estimates for all five macronutrients (N, P, K, Ca, Mg) in coarse roots in tropical forests.

We hypothesise that sapwood generally holds higher concentrations than heartwood, as higher nutrient concentrations are required to maintain living tissue, and inorganic nutrients are normally supplied via transpirational xylem stream (Pfanz, 2007).

We address the following research questions:

Q1) How do wood nutrient concentrations vary within a trunk cross-section (radially)?

Q2) Is there evidence for nutrient resorption or accumulation in wood during sapwood senescence?

Q3) How do wood nutrient concentrations vary along the length of the tree (vertically)?

Q4) How does wood density vary vertically, and how does it correlate with wood nutrient concentration and total tree height?

MATERIALS AND METHODS

Site description:

The study site is located in the state of Sabah, Malaysian Borneo (4°43′ N, 117°35′E). The vegetation is a mixed dipterocarp lowland rainforest, which is the most extensive forest type in Malaysian Borneo (Palmiotto et al., 2004). The family Dipterocarpaceae reaches the highest density with ten genera and about 270 species described (Burghouts, 1993). Soils are acrisols and luvisols (WRB classification), developed over the underlying bedrock of predominantly mudstone and sandstone (Acres, 1975). The climate is aseasonal with mean annual temperature of ca. 27.0 °C and annual precipitation of 3500 mm (Imai et al., 2012b). The study is part of the Stability of Altered Forest Ecosystems (SAFE) Project, one of the world's largest experiments in human-modified forest landscapes, which examines the impacts of logging and forest conversion to oil palm on biodiversity, ecosystem functioning and productivity (Ewers et al., 2011). The SAFE site has previously been logged at different intensities (Struebig et al., 2013).

The study took place in a logging site where direct felling was being conducted within the Benta Wawasan (concession holders) area. The trees sampled for the study were felled as part of concessional logging operations due to forest conversion to oil palm plantation under the Yayasan Sabah (landowners) Forest Concession.

Sampling of tree components:

Tree components were sampled in August 2014. Thirty trees ≥ 10 cm diameter at breast height (DBH), which consisted of 10 tree species with three replicates were selected in the study site (Table 4.1). Within each tree, 14 different locations were

sampled (Fig. 4.1 and 4.2). Collected voucher specimens of the trees were verified at the herbarium of the Forest Research Centre, Sabah Forestry Department in Sepilok, Sabah.

Table 4.1 The list of sampled tree species grouped by successional types (n = 30; 10 species with three replicates)

Family	Genus	Species	Height range (m)	DBH[a] range (cm)	Species code
Dipterocarps					
Dipterocarpaceae	*Parashorea*	*P. malaanonan*	14.0 – 28.7	12.2 – 44.1	**DP.m**
Dipterocarpaceae	*Shorea*	*S. johorensis*	14.7 – 23.4	13.9 – 41.8	**DS.j**
Dipterocarpaceae	*Shorea*	*S. leprosula*	16.5 – 19.4	24.1 – 27.2	**DS.l**
Dipterocarpaceae	*Shorea*	*S. micans*	11.3 – 15.4	11.8 – 13.2	**DS.m**
Dipterocarpaceae	*Shorea*	*S. parvifolia*	12.4 – 16.5	11.7 – 20.1	**DS.p**
Other non-pioneers					
Fagaceae	*Lithocarpus*	*L. leptogyne*	9.7 – 20.6	17.2 – 24.8	**FL.l**
Malvaceae	*Pentace*	*P. laxiflora*	12.0 – 18.6	12.5 – 25.2	**MP.l**
Pioneers					
Cannabaceae	*Trema*	*T. orientalis*	13.8 – 17.7	30.2 – 33.3	**CT.o**
Euphorbiaceae	*Macaranga*	*M. pearsonii*	12.8 – 19.3	23.4 – 26.4	**EM.p**
Rubiaceae	*Neolamarckia*	*N. cadamba*	7.2 – 14.2	22.5 – 30.8	**RN.c**

Successional types were classified according to Köhler et al. (2000), Davies and Semui (2006) and Saner et al. (2012).

[a]Diameter at breast height (1.30 m).

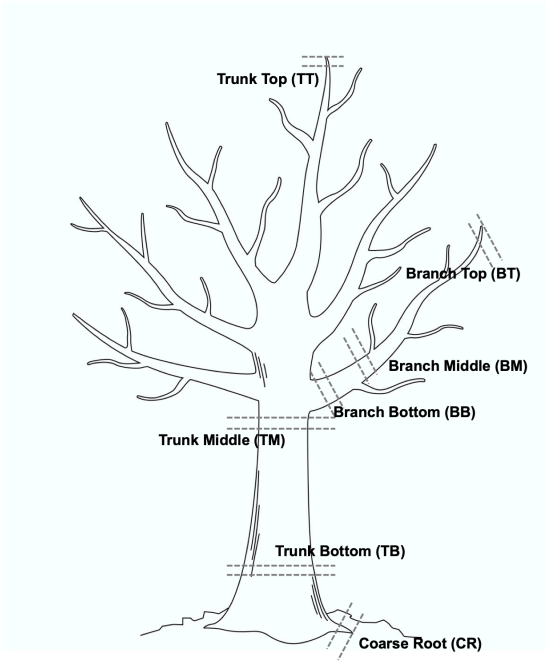


Figure 4.1 Sampled vertical woody components.

Three positions of trunk were sampled: trunk bottom (TB) (just below the breast height of 1.3 m off the ground), trunk middle (TM) (just below the lowest major branch), and trunk top (TT) (at the tip of the trunk). The lowest branch from the ground was sampled, which were divided into three locations: branch bottom (BB) (the closest location to the trunk), branch middle (BM) (where the lowest sub-branch emerges), branch top (BT) (the tip of the branch). Coarse root (CR) was excavated and sampled from the soil within a radius of 0.5 m from the trunk.

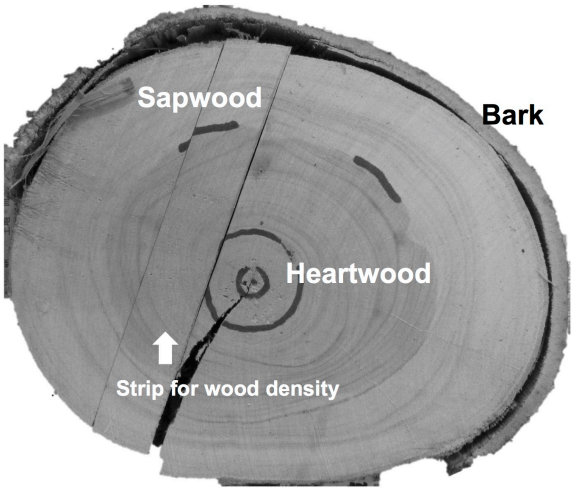


Figure 4.2 Sampled radial woody components.

Trunk bottom (TB) and trunk middle (TM) (see Fig. 4.1) were portioned to three sections: bark, sapwood and heartwood. A wood strip across sapwood and heartwood was separated for wood density (WD) testing. Measurements of WD were performed from one end to the other end of the wood strip depending on the strip size (maximum five measurements).

Selection of tree species:

To characterise the species composition in the study area, tree censuses were conducted during 2011 and 2012, and 1,580 trees (≥ 10 cm DBH) of 405 species were identified in five 1-ha logged-plots at the SAFE Project area (Riutta et al., 2018, Both et al., 2019). The species sampled for this study represented 25% of total number of individual stems, including most abundant species by ranking: *Macaranga pearsonii* (17% abundance), and some of dominant species: *Parashorea malaanonan* (2% abundance) and *Neolamarckia cadamba* (1% abudance).

Dipterocarpaceae is the most dominant family in Borneo (Palmiotto et al., 2004), accounting for 19% of the stems in the study area, and a half of our sampled trees

belongs to this family. This family is also favoured for logging. *Macaranga pearsonii*, *Neolamarckia cadamba* and *Trema orientalis* are considered as pioneer species (Table 4.1) (Davies and Semui, 2006, Saner et al., 2012). Hence, we sampled a broad taxonomic range from light-demanding pioneer to shade-tolerant late-successional species.

Although in most cases the three replicates of each species were of similar size (Table 4.1), standardising the DBH size-class within replicates was not feasible due to high species diversity in the study site.

Sampled trees had no visible damage (e.g. no insect damage, chlorotic leaves and bent stems). All measurements (the number of branches, diameters and length of all sampled locations) were conducted using a measuring tape within hours after the sampled trees were felled. Directly following felling, sampled woody components were cut using a chainsaw. The samples were brought to the chemistry laboratory of the Forest Research Centre in Sepilok, Sabah. Trunk samples were partitioned to three sections: bark, sapwood and heartwood (Fig. 4.2).

Bark is defined as all tissues external to the vascular cambium. The analysed bark layer comprised outer bark which was composed of dead cells known as periderm, and inner living bark including secondary phloem, cortex and phelloderm (Evert et al., 2006, Rosell et al., 2015, Rosell, 2016). The vascular cambium was often only one or two cells thick, and required a microscope to see it well.

The outermost wood layers containing living cells (xylem) are referred to as sapwood, whereas the inner wood layers containing no living cells are referred to as heartwood (Bamber and Fukazawa, 1985, Hillis, 1987). The collected trunk disk was divided into sapwood and heartwood based on a distinguishable colour difference after mechanical sanding. If there was no clear colour difference, the section of the rim of the disk was used as a sapwood sample and the wood around the pith as a heartwood sample (Fig. 4.2).

Due to the absence of colour boundary between sapwood and heartwood in most branch and coarse root samples, they were disaggregated into wood and bark only. The twig tips of sampled branches (less than 2 cm diameter) were not debarked.

Chemical analyses:

Woody samples for the chemical analysis totaled 420 samples (10 species × 3 replicates × 14 sampled locations within a tree). Concentrations of five macronutrient elements (N, P, K, Ca and Mg) and carbon (C) in each individual component were quantified at the chemistry laboratory of the Forest Research Centre, Sepilok. First, all samples were oven dried at 50 °C to constant weight for five days, and were then ground with a Thomas Wiley Mill to pass through a 100-mush (212-μm) sieve.

Most of the lab analysis protocols are described in more detail in Majalap and Chu (1992), and a summary of the methods used is as follows. Each sample was digested

following the sulphuric acid-hydrogen peroxide-lithium sulphate digest procedure for vegetation described in Allen (1989). Phosphorus in the digest was determined using the molybdenum-blue method described in Anderson and Ingram (1993) and read at 880 nm on a spectrophotometer (HITACHI UV-VIS, Tokyo, Japan), while K, Ca and Mg contents were measured on an atomic absorption spectrophotometer (GBC Scientific Equipment, Victoria, Australia). Total C and N contents (as total element contents) were determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany).

Estimation of wood density (WD):

Wood density was measured by following the procedure ISO 3131:1975 (E) Wood -- Determination of Density for Physical and Mechanical Tests. Wood density was defined as the oven-dry mass per unit volume of green wood cube (tangent 20 mm × axial 20 mm × radial 20 mm length), given in g cm^{-3}. Dry mass was measured after oven drying at 103±2 °C until the dry mass was stabilised.

Measurements of WD were performed from one end to the other end of the wood strip depending on the strip size (maximum five measurements; see Fig. 4.2) at two locations in trunk: trunk bottom (TB) and trunk middle (TM).

Estimation of wood nutrient resorption rate:

Wood nutrient *(x)* resorption rate (%) was computed for each species as

$$xR = \left(1 - \frac{x_{heartwood}}{x_{sapwood}}\right) \times 100 \quad \text{(Eq. 1)}$$

where *x* is an element of either N, P, K, Ca, Mg or C, *x*R is the *x* resorption rate, $x_{sapwood}$ is the species mean *x* concentration in sapwood, $x_{heartwood}$ is the species mean *x* concentration in heartwood.

Statistical analyses:

For each measured element, we used liner mixed-effects models to test whether wood nutrient concentration varied both radially and vertically. We created a separate model for each nutrient. In each model, the response variable was the nutrient concentration, the fixed effect was either the vertical location (trunk bottom, TB vs. trunk middle, TM) or the radial location (bark, sapwood or heartwood) and the tree species and the individuals within each species were included as nested random effects. Wood nutrient concentrations were log-transformed before linear mixed-effects models to meet the assumption of normality of errors. We also used linear mixed-effects models to test whether wood resorption varied between species groups (dipterocarps, other non-pioneers and pioneers, Table 4.1). We created a separate model for each nutrient. In each model, the response variable was the resorption rate, the fixed effect was the species group and random effect was tree species. Tukey HSD pot-hoc test was used to determine which pairs differed significantly, and the Bonferroni correction was performed to account for multiple comparisons.

We used a major axis regression to examine the relationship between wood density

at the trunk bottom and trunk middle. Statistical analyses were performed in the R programming language version 4.0.4 (R Core Team, 2021) and the packages 'ggplot2' (Wickham, 2016), 'lme4' (Bates et al., 2015), and 'smatr' (Warton, 2012).

RESULTS

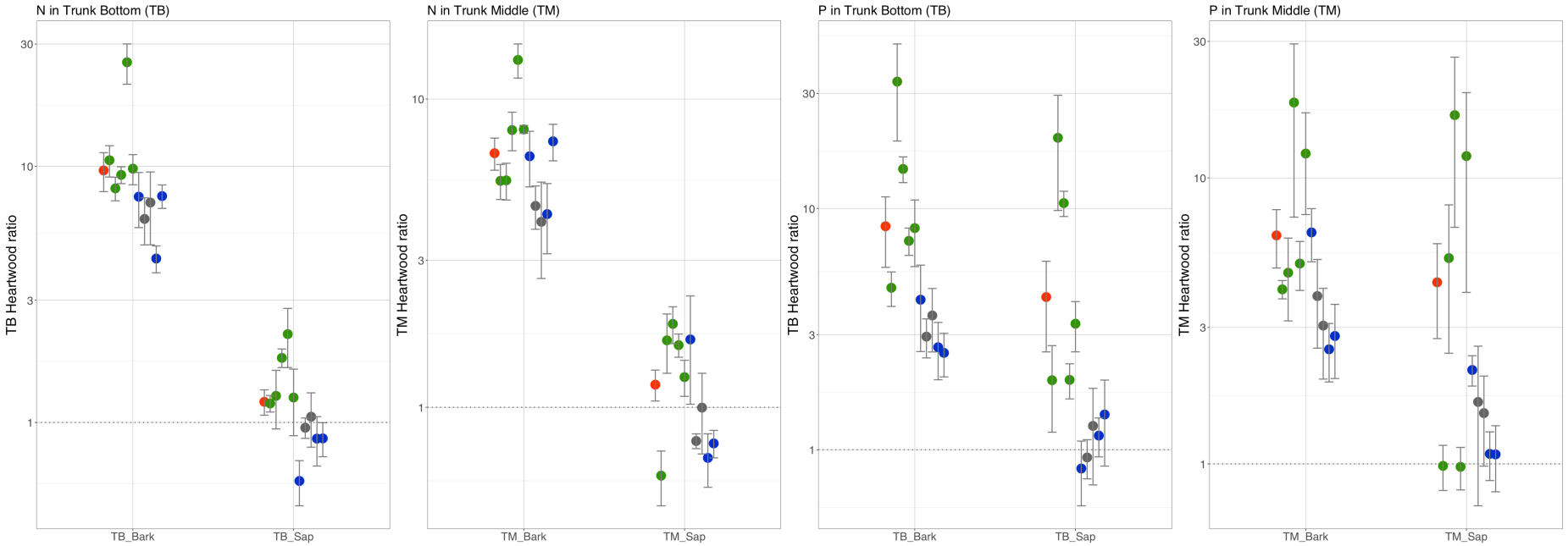
Variation in nutrient concentrations between bark and wood

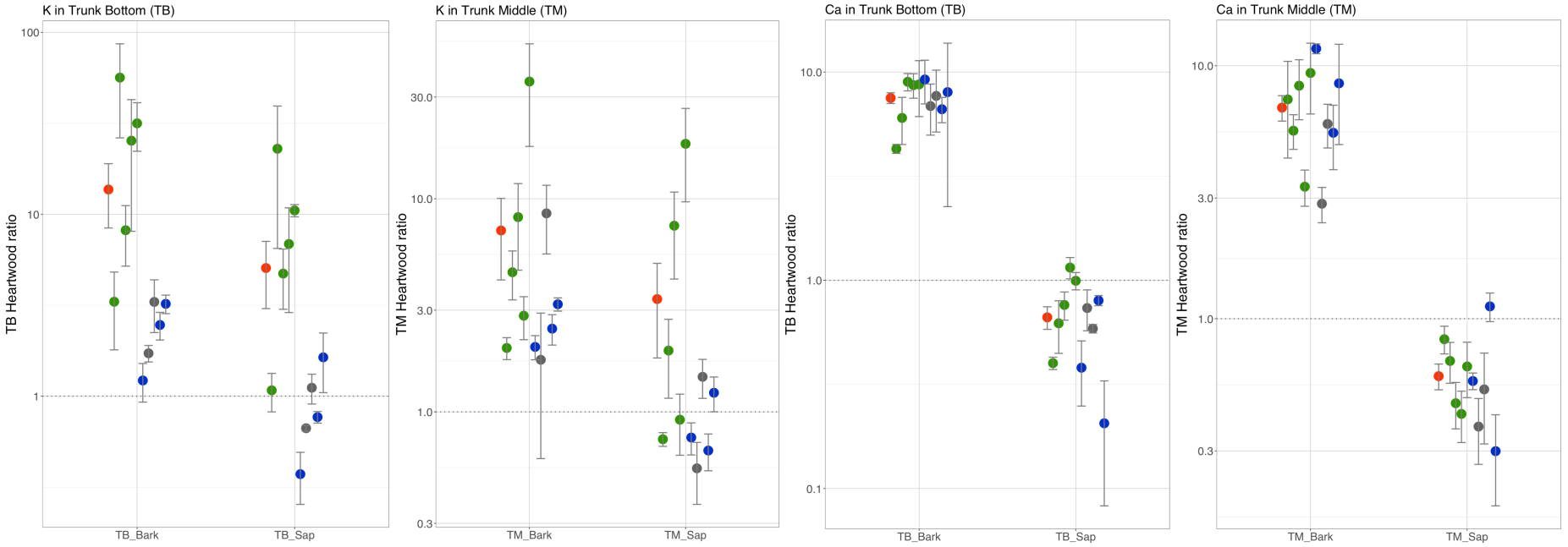
Bark had substantially higher nutrient concentrations than sapwood or heartwood (Fig. 4.3, Fig. S4.2, Table 4.2, Table S4.2) in almost all sampled trees. The bark to trunk heartwood mean ratio was 2.9-13.7 depending on the nutrient. For N, the mean bark to heartwood ratio across species was 9.63±1.67 at the bottom of the trunk and 6.67±0.80 in the middle of the trunk. For P, the corresponding ratios were 8.44±2.74 and 4.29±1.75. This large change in the ratios between the bottom of the trunk and the middle of the trunk was driven by the sharp decline in the bark P concentration from trunk bottom to trunk middle while heartwood P concentration showed little vertical variation (Fig. 4.4, Table S4.2).

Table 4.2 Mean ratio (± 1 SE) between nutrient and carbon concentrations in bark, sapwood and heartwood in the trunk bottom (TB) and trunk middle (TM);

the first component divided by the second component in each case. The values are averages of the ten studied tree species (see Table 4.1). The values in bold indicated significant differences ($p<0.05$), i.e., they are significantly different from the expectation of a 1:1 ration for each nutrient, tested using linear mixed-effects models with the Tukey HSD post-hoc test. The p-values were Bonferroni corrected to account for multiple comparisons.

	N	P	K	Ca	Mg	C
TB bark : TB heartwood	**7.42±0.94**	**3.48±0.75**	**2.34±0.55**	**6.12±1.00**	**2.14±0.53**	**0.96±0.01**
TB bark : TB sapwood	**7.33±0.78**	**2.29±0.52**	**2.71±0.34**	**11.66±1.70**	**4.09±0.91**	**0.95±0.01**
TM bark : TM heartwood	**5.23±0.76**	**3.50±0.61**	**2.49±0.45**	**4.93±0.87**	**1.86±0.43**	**0.97±0.01**
TM bark : TM sapwood	**5.32±2.03**	**2.11±0.95**	**2.72±1.14**	**10.39±5.00**	**4.74±2.62**	**0.97±0.09**
TB heartwood : TB sapwood	0.99±0.14	0.66±0.23	1.16±0.27	1.90±0.29	1.91±0.46	0.99±0.005
TM heartwood : TM sapwood	1.02±0.17	0.60±0.11	1.09±0.19	2.11±0.44	**2.55±0.72**	1.00±0.004


N in Trunk Bottom (TB)
TB Heartwood ratio
30
10
3
1
TB_Bark
TB_Sap
N in Trunk Middle (TM)
TM Heartwood ratio
10
3
1
TM_Bark
TM_Sap
P in Trunk Bottom (TB)
TB Heartwood ratio
30
10
3
1
TB_Bark
TB_Sap
P in Trunk Middle (TM)
TM Heartwood ratio
30
10
3
1
TM_Bark
TM_Sap


K in Trunk Bottom (TB)
TB Heartwood ratio
100
10
1
TB_Bark
TB_Sap
K in Trunk Middle (TM)
TM Heartwood ratio
30.0
10.0
3.0
1.0
0.3
TM_Bark
TM_Sap
Ca in Trunk Bottom (TB)
TB Heartwood ratio
10.0
1.0
0.1
TB_Bark
TB_Sap
Ca in Trunk Middle (TM)
TM Heartwood ratio
10.0
3.0
1.0
0.3
TM_Bark
TM_Sap

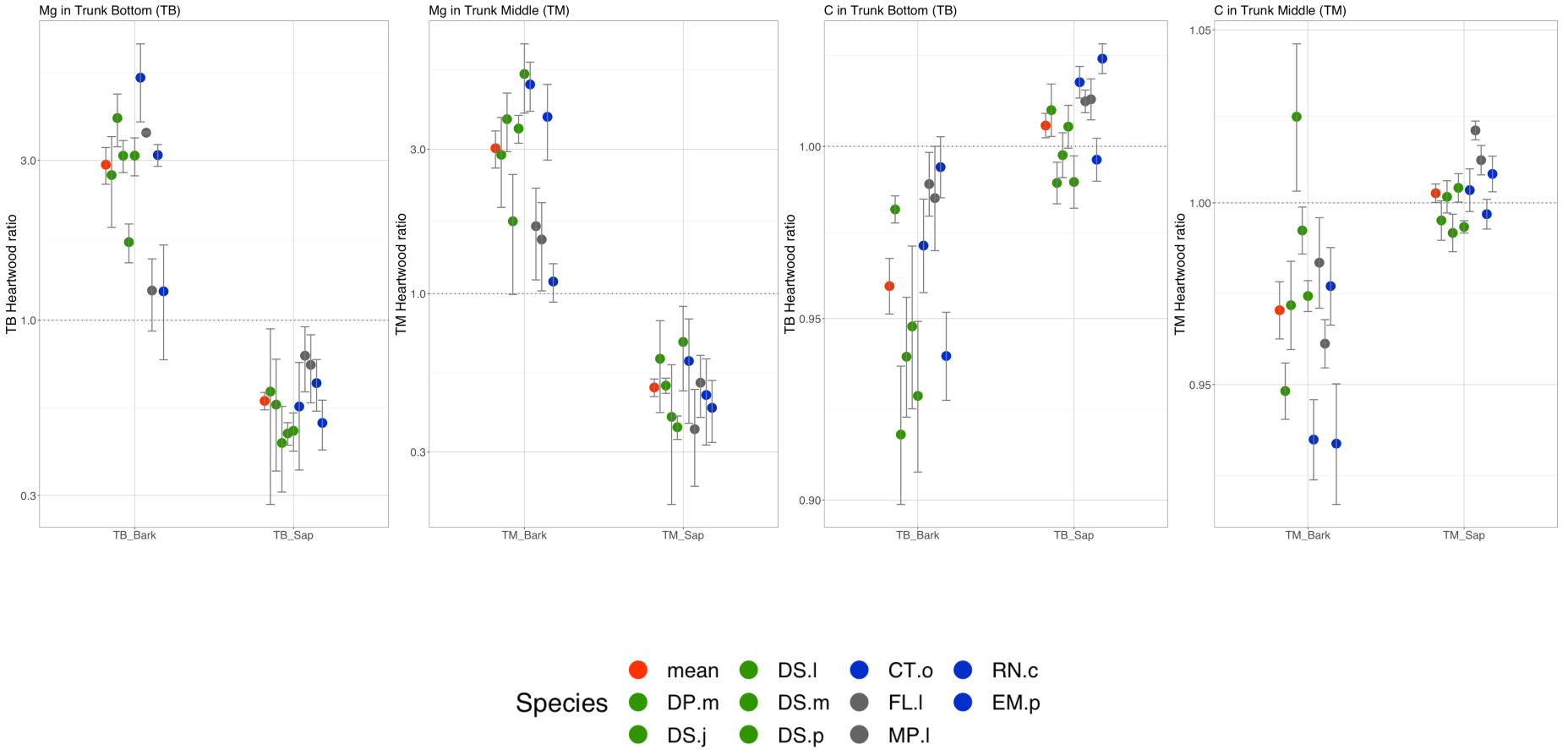
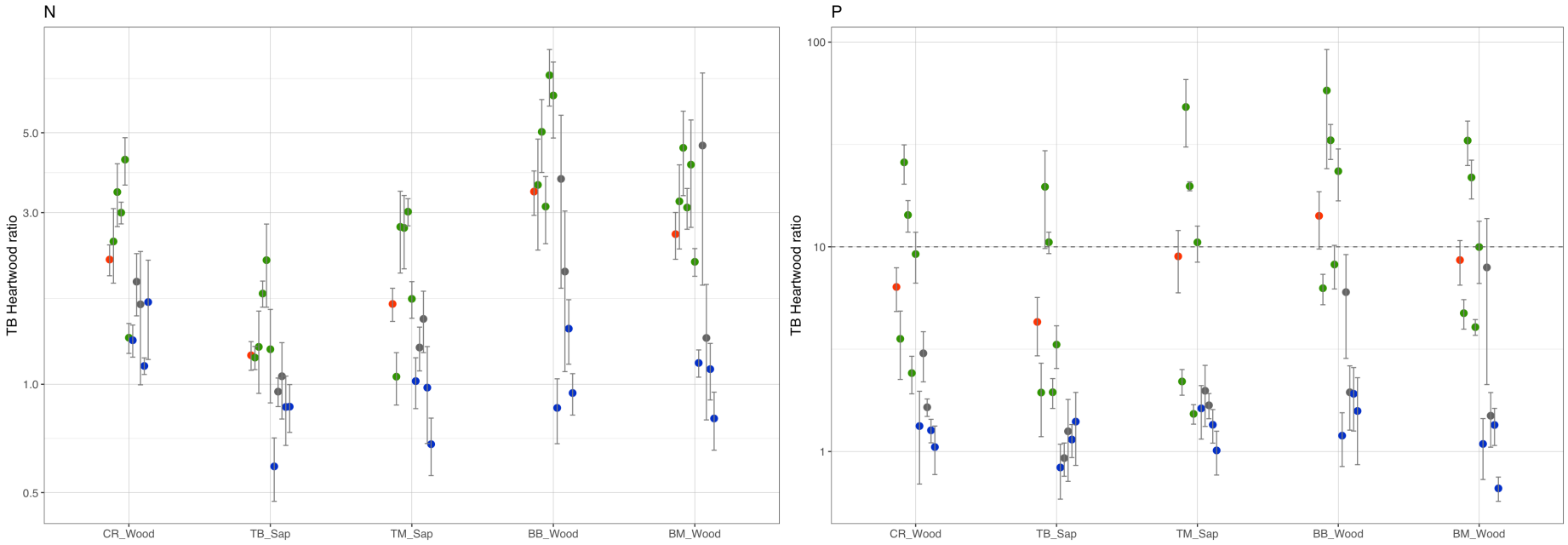
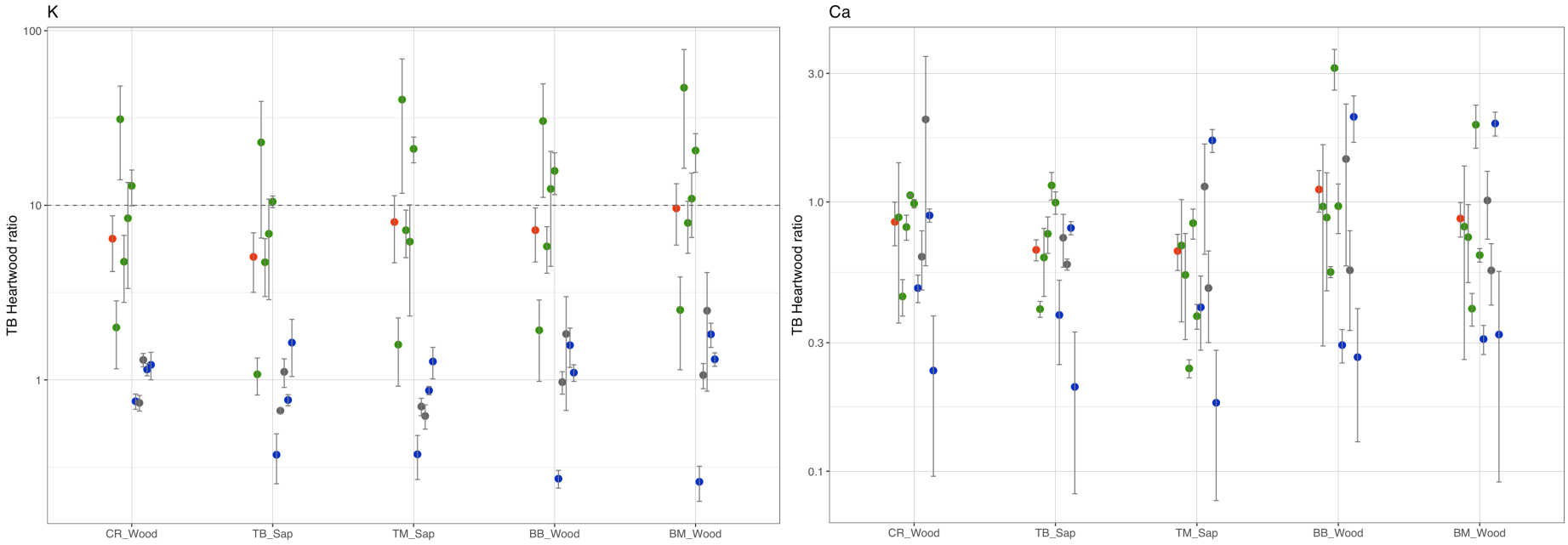


Figure 4.3 Nutrient and carbon concentrations in bark and sapwood relative to heartwood in trunk bottom (TB) and trunk middle (TM) (as a ratio).

Values are mean (±SE). of each species (*n* = 3) (see Table 4.1, Table S4.3). The red point indicates total mean across species (n=10), the green, grey abd blue points indicate Dipterocarp, non-pioneer and pioneer species, respectively. Note the difference scales and log transformation of the y axes.


N
P
TB Heartwood ratio
5.0
3.0
1.0
0.5
100
10
1
CR_Wood
TB_Sap
TM_Sap
BB_Wood
BM_Wood


K
TB Heartwood ratio
100
10
1
CR_Wood
TB_Sap
TM_Sap
BB_Wood
BM_Wood
Ca
TB Heartwood ratio
3.0
1.0
0.3
0.1
CR_Wood
TB_Sap
TM_Sap
BB_Wood
BM_Wood

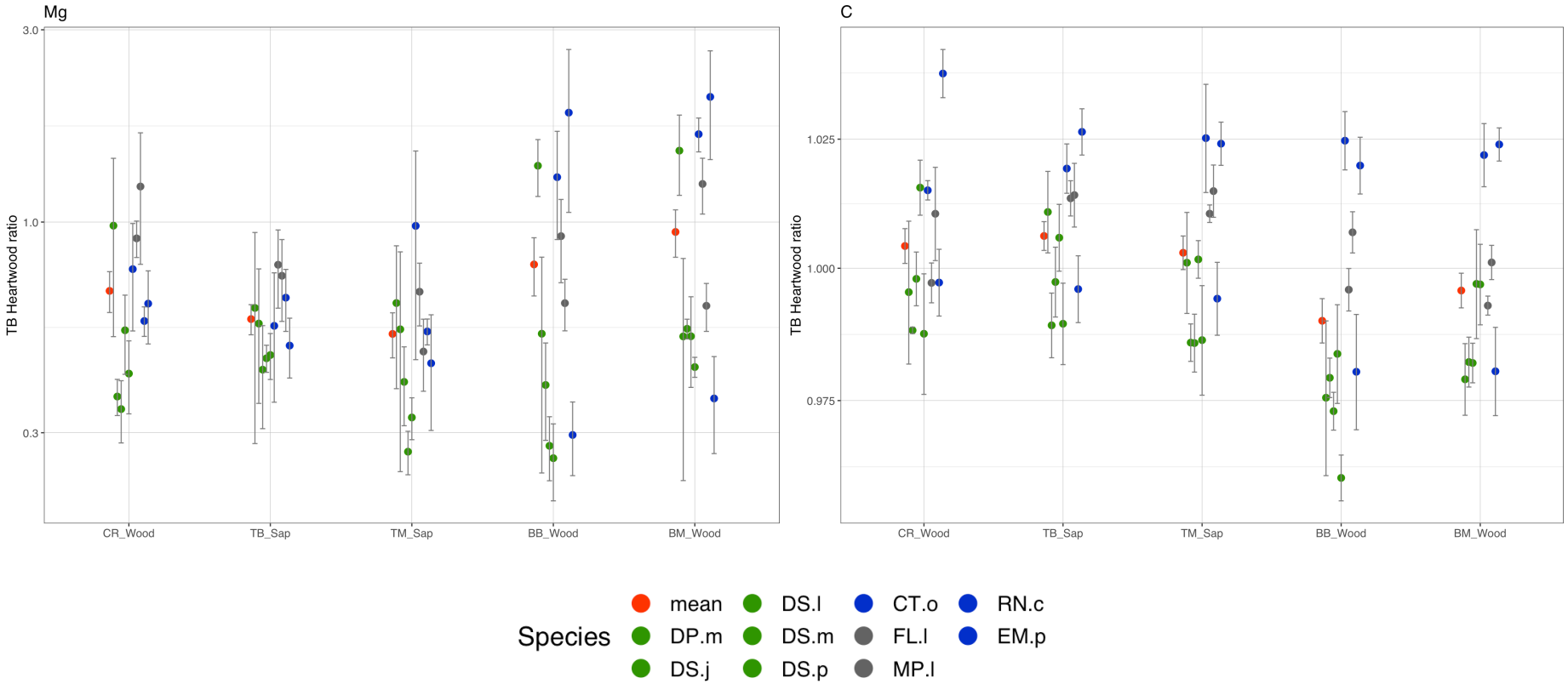


Figure 4.4 Nutrient and carbon concentrations in woody components relative to heartwood in trunk bottom (TB) (as a ratio) along the length of the tree.

Woody components on x axis are coarse root (CR) wood, trunk bottom (TB) sapwood, trunk middle (TM) sapwood, branch bottom (BB) wood, and branch middle (BM) wood (see Fig. 4.1 and 4.2). Values are mean (±SE) of each species (*n* = 3). The red point indicates total mean across species (n=10), the green, grey and blue points indicate Dipterocarp, non-pioneer and pioneer species, respectively. Note the different scales of the y axes.

The dipterocarp family had particularly large concentrations in bark (Fig. 4.3). *Shorea micans* had among the highest N ratio between bark and heartwood at the lowest trunk level (25.47±4.56). *Shorea johorensis* showed among the highest P ratio between bark and heartwood (33.57±14.53). *Shorea johorensis* also had exceptionally high K ratio between bark and heartwood (56.43±30.13). While *Trema orientalis*, a pioneer species, had higher Ca ratio between bark and heartwood (11.68±0.53), Ca and Mg ratios were generally more constrained across species. Across elements, intra-specific variation was large particularly for dipterocarps.

Wood resorption from heartwood to sapwood

The mean concentrations across species indicated no significant difference between sapwood and heartwood (Table 4.2). We examined this further by dividing the sampled species into taxonomic and successional groups (Table 4.1). The ratio of sapwood to heartwood concentration varied from below to above one, depending on the nutrient and tree species (Fig. 4.3) The former pattern suggests accumulation in heartwood, whereas the latter indicates wood resorption during sapwood senescence (Bamber and Fukazawa, 1985, Hillis, 1987, Smith and Shortle, 1996, Saka and Mimori, 1994). The difference in the nutrient concentrations between sapwood and heartwood was larger for the dipterocarp species than for the other species for N, P and K (Fig. 4.3). While dipterocarps had consistently higher nutrient concentrations in sapwood than in heartwood, the other species showed either smaller differences or in several cases

lower concentrations in sapwood.

A difference between sapwood and heartwood by dipterocarp species suggested wood resorption at the rates of 25.3±7.1% (N), 62.7±11.9% (P), and 56.2±12.5% (K) respectively at the bottom of trunk (TB) (Table S4.3), which was significantly higher than the resorption rate of the non-dipterocarps species for N (p=0.011) and P (p=0.005), and marginally significant for K (p=0.057). At the middle of trunk (TM), the resorption rates in dipterocarps declined compared to the bottom of trunk at 10.7±13.6% (N), 41.9±13.0% (P) and 20.4±15.2% (K), respectively. In contrast, Ca and Mg tended to accumulate in heartwood in 9 out of 10 species (Ca), and all species (Mg), with no difference between dipterocarps and non-dipterocarps (p=0.265 and p=0.080 for Ca and Mg, respectively).

Vertical variation in nutrient concentrations

There was no significant variation in nutrient concentrations between trunk bottom and trunk middle in bark, sapwood or heartwood for most of the nutrients (Table S4.2). The main exception was bark P concentration, which was lower in the trunk bottom compared to the trunk middle (p=0.005).

Across the whole length of the tree, from coarse roots through trunk wood to branch bottom and branch middle, there was a trend in wood nutrients, with the lowest concentrations in the trunk, increasing both towards coarse roots and branches, with

significant differences found for N, P and C concentrations (Fig. 4.4, Table S4.1). Branch bottom (BB) had exceptionally high N, P and K relative to other components. The difference among species was, however, considerable. While there was extraordinarily large vertical variation in the dipterocarp family (green lines in Fig. 4.4), pioneer species such as *Macaranga pearsonii* and *Trema orientalis* showed nearly no vertical variation in N, P and K concentrations. Vertical variation was modest for Ca and Mg. Note that this comparison was done using trunk sapwood, as we consider coarse roots and branches to consist of mostly sapwood.

In contrast to the vertical variation in wood concentration, there were significant differences between trunk bark, branch bark and coarse root bark in P, K and Ca (Fig. S4.2, Table S4.2).

Wood density

There was a strong correlation between TB and TM density (Fig. 4.5). The slope of the Major Axis Regression between TB and TM density was 0.90, with 95% confidence intervals of 0.80 and 1.02, indicating little or no difference between WD in TB and TM.

There were no differences in the mean wood density between species groups ($p=0.437$). There were, however, high variability among species: *Shorea micans* had exceptionally high WD: 0.94±0.01 g/cm^3 in TB and 0.83±0.02 g/cm^3 in TM respectively, followed by *Lithocarpus leptogyne* (Fig. 4.5). In contrast, some pioneer species such

as *Macaranga pearsonii* and *Trema orientalis* had soft wood. *Macaranga pearsonii* had the lowest density of 0.33±0.01 g/cm^3 in TB and 0.30±0.01 g/cm^3 in TM respectively.

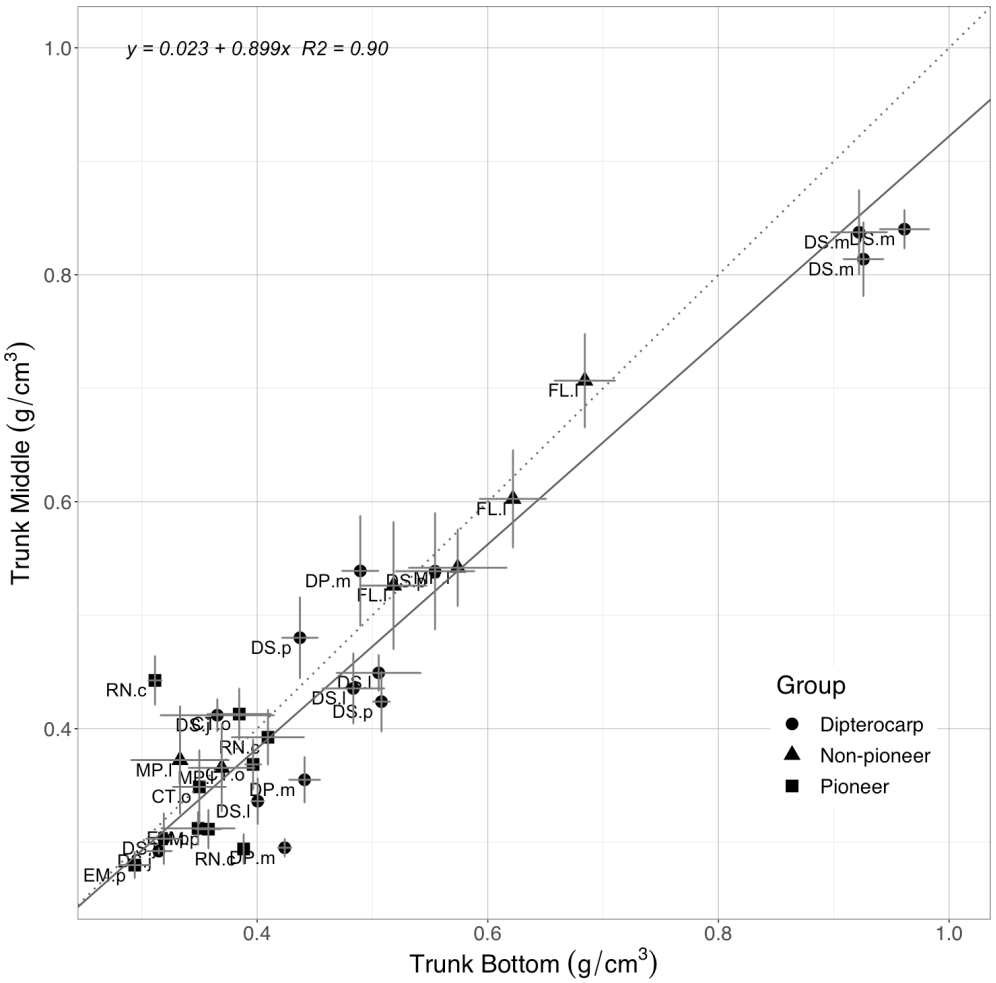


Figure 4.5 Linear relationship of wood density between trunk bottom and trunk middle.

We sampled ten species (grouped into dipterocarps, other non-pioneers and pioneers) with three replicate trees. Species codes are listed in Table 4.1. Each data point is the mean (±SE) of an individual tree with two to five samples taken per tree. The continuous line shows the fit of the major axis regression and the dashed line is the 1:1 relationship.

DISCUSSION

Radial variation

The high nutrient concentrations in bark (Fig. 4.3) may be attributed to bark anatomy, in which inner bark acts as nutrient storage. Bark has an inner living part and outer part composed of dead cells, derived from different lateral meristems (Evert et al., 2006). Inner bark contains secondary phloem, translocating photosynthates from the leaves to the rest of the plant (Ryan and Asao, 2014), as well as a large proportion of living parenchyma which stores water and photosynthates (Scholz et al., 2007, Romero, 2014). A study on bark thickness shows especially large proportions of inner bark in tropical tree species (Rosell, 2016), and the storage is likely to be determined by the amount of inner bark (Rosell and Olson, 2014). The N_2-fixing tropical trees (*Fabaceae*), for example, accumulate bark storage proteins in secondary phloem and xylem parenchyma (Hao and Wu, 1993), whereas temperate tree species store N derived from breakdown of leaf protein as bark storage proteins during winter and fertilizer to support new growth in spring (Millard, 1996).

While N, P and K concentrations vary among species, Ca concentrations in bark were substantially high relative to sapwood and heartwood for all species (Fig. 4.3). High Ca concentrations in bark has also been reported in some temperate tree species (Trockenbrodt, 1995, Österås and Greger, 2006). Calcium is immobile in the phloem

and is mainly accumulated in the cell walls, and it later becomes no longer available metabolic processes in the symplast. Excess Ca ions can be deposited as Ca oxalate crystals in the bark or phloem, the cell walls of which serve as a Ca reservoir (Fromm, 2010).

Calcium cycling in forests may be susceptible to biomass removal and disturbance as Ca accumulates in woody biomass (McGrath et al., 2001). Several studies find that repeated timber harvesting cause the substantial losses of soil Ca due to removed Ca-rich woody biomass from the site (Brouwer and Riezebos, 1998, Zech and Drechsel, 1998, Spangenberg et al., 1996, Huntington et al., 2000). In Sabah, the loss of Ca via leaching exceeds the annual input of Ca via wet deposition (Grip et al., 1994), which is below 2kg ha^{-1} yr^{-1} (Nykvist, 2000). The harvesting of stem wood and bark results in the loss of 19% of the total Ca in the ecosystem and soil to 50 cm depth in Sabah (Nykvist, 1997). Sustainable forestry is not possible unless liming, fertilization or wood ash is applied (Nykvist, 2000).

Sapwood and heartwood are anatomically different. Inner sapwood rings are eventually converted to heartwood, which no longer contains living cells, often has vessels blocked with tyloses and accumulates secondary compounds (Bamber and Fukazawa, 1985, Hillis, 1987). We found substantial decreases in N, P and K concentrations in heartwood relative to sapwood in many species, notably the dipterocarps, but not in most other species (Fig. 4.3). These dipterocarp results are consistent with a global meta-analysis of 71 angiosperm species by Meerts (2002) that

N, P and K concentrations are generally lower in heartwood. These higher concentrations in sapwood, however, may originate either from the structural wood tissue or the nutrients in the liquid component of the xylem, which might have been retained in the samples during the drying process or both.

In contrast, we found concentrations of Ca and Mg are slightly higher in heartwood (Fig. 4.4). Such results may reflect Ca accumulation in the form of crystals (Hillis, 1987). Frangi et al. (2005) also report that Ca and Mg in sapwood tend to be low in boreal montane forests, whereas the global meta-analysis shows the complex pattern of these cations, which could be explained by phylogenetic constraints (Meerts, 2002).

As the sapwood and heartwood nutrient concentrations differ, sapwood to heartwood ratio is an important variable to include when quantifying whole-tree nutrient budgets.

Wood resorption

Sapwood had substantially higher N, P and K concentrations than heartwood in dipterocarp species, but not in other families. For dipterocarps, our results provide empirical support for a hypothesis that resorption from woody stems occurs during the conversion of sapwood into heartwood. This suggests an efficient nutrient conservation mechanism of N, P and K in dipterocarps, which overall have low nutrient concentration in wood (Table S4.3).

Secondary compounds tend to be located in heartwood, while starch, soluble sugars, amino acids and nutrient elements such as N, P and K are resorbed from senescing sapwood rings (Bamber and Fukazawa, 1985, Hillis, 1987, Smith and Shortle, 1996, Saka and Mimori, 1994). Conversely a large amount of Ca and Mg accumulates in the cell wall, which is less mobile than N, P and K in the xylem (Cutter and Guyette, 1993, Marschner, 1995, Meerts, 2002). There is a similar pattern of how much each element is resorbed from leaves and wood, despite the considerable difference in chemical composition of leaf and wood tissues (Aerts, 1996, Schlesinger and Bernhardt, 2013). Phosphorus in the form of adenine nucleotides, particularly, is largely resorbed during sapwood senescence in a deciduous tree (Magel and Höll, 1993). Although there are no direct studies on wood resorption in tropical forests, resorption of P from sapwood appears to be predominant in Panama as wood P was lower in the inner annulus than the outer annulus (Heineman et al., 2016). In the analysis of 40 subarctic vascular species, resorption by fine stems (< 3 mm diameter) is also substantial for N and P (Freschet et al., 2010).

Vertical variation

The magnitude of wood mean nutrient concentrations was ordered by N > Ca > K > Mg > P, respectively, in which the pattern was consistent with a recent study in Panama (Heineman et al., 2016). For most species there was negligible variation along the

length of the main trunk, suggesting that wood sample collection near the bottom of the tree is usually representative of entire main trunk, where the bulk of woody biomass is found.

Branches, however tended to show higher nutrient concentrations than the main trunk (Fig. S4.1). Sampling of outer branches may be in some cases easier for wood trait analyses than sampling of main trunk (e.g. when leaf traits are being collected). Given highly varied concentrations along the length of the tree, particularly among dipterocarp species (green lines in Fig. S4.1), our findings suggest that it is problematic accurately estimate to the whole tree wood concentrations from branch samples.

Wood density

Our results suggested radial variation of WD was small (Fig. 4.5). Results from previous studies are mixed. There is substantial radial variation in WD of tropical pioneer angiosperm species, which have greatly lower wood density near the pith (Wiemann and Williamson, 1988). On the contrary, heartwood densities were reported to be substantially higher than sapwood densities in Amazonia (Woodcock and Shier, 2002, Patiño et al., 2009). This pattern is associated with changes in chemical deposition in heartwood (Chave et al., 2009).

Although our study did not examine coarse root WD, they tend to be lower than stems

(Pratt et al., 2007). In our study, there was no relationship between wood nutrient concentrations and WD (Fig. S4.3).

In previous studies, both a positive correlation for N in Panama (Martin et al., 2014) and no relationship in Uganda (Becker et al., 2012) have been observed between wood N and WD.

In a recent study in Panama, while WD significantly declined as wood P concentration increased at the species level, WD was not significantly associated with wood N, K, Ca and Mg concentrations (Heineman et al., 2016). Parenchyma cells in woody tissues store chemical compounds (Carlquist, 2007) such as N in the form of free amino acids (Kato et al., 1984), and maintain higher WD than other cell constituents (Taylor, 1969). This explains why wood N may be positively correlated with WD (Poorter, 2008, Chave et al., 2009).

In addition, the patterns of WD and wood nutrient concentrations are interlinked to tree height. For example, maximum tree height in the analysis of 42 tree species in Bolivia had a relationship with anatomical traits such as WD (negative), vessel diameter (positive) and hydraulic conductance (positive) (Poorter et al., 2010).

The dataset in our study did not have a sufficient DBH range within species (Table 4.1) to analyse size-class changes in wood nutrient concentrations. To our knowledge, there is no size-class comparison study on wood nutrients, while Martin et al. (2013) directly measure wood holocellulose, lignin and C concentrations at a large tree

against sapling size classes in Panama. Lignin and C are generally higher in saplings than conspecific large trees, suggesting the importance of ontogenetic changes in wood chemical traits. Feldpausch et al. (2004) report that wood concentrations of N and P decrease with secondary forest age in Amazonia, with an average reduction of 50% (N) and 60% (P) from the youngest to the oldest forests. However wood core measurements in that study included bark, which may lead to overestimation in young stands (Feldpausch et al., 2004), because saplings have a higher proportion of bark than mature trees.

CONCLUSION

To the best of our knowledge, this study is the first to examine in detail the distribution of macronutrients across woody components within whole tropical trees. Since the only available published meta-analysis for wood nutrient concentrations to date is deficient in tropical species data (Meerts, 2002), our study provides essential information, considering the extensive number of samples: 420 woody components of 30 trees for the observation of six elements.

As ecosystem nutrient stocks are often calculated using the allometry in whole-plant stoichiometry (Elser et al., 2010), our results provide new insights into nutrient variation within a whole tree to improve such estimations. Wood nutrient concentrations also affect decomposition rates of coarse woody debris. Wood

decomposition, especially following disturbance, may have a large contribution to soil C and nutrient dynamics (Martin et al., 2014).

Bark is known to host higher concentrations of C and N as compared to other woody tissues (Wetzel and Greenwood, 1989, Jenkins et al., 2003), and our results present the same pattern in P, K, Ca and Mg. As several studies report Ca deficiency after logging in Sabah and elsewhere (Grip et al., 1994, Nykvist, 1997, Nykvist, 1998, Nykvist, 2000, Brouwer and Riezebos, 1998, Spangenberg et al., 1996, Zech and Drechsel, 1998, Huntington et al., 2000), we suggest debarking process during logging operations helps recycle nutrients within forest ecosystems, which could be one of the nutrient conservation practices for foresters and conservationists.

Our results also provided empirical support for wood resorption during sapwood senescence, which is specific to dipterocarp family. This suggests an efficient conservation mechanism of N, P and K, and that generally lower wood nutrient concentrations in dipterocarps are largely compensated by wood resorption.

Wood chemical traits need to be evaluated in concert with other functional traits such as species-level growth and mortality rates to support the conceptual framework of WES (Chave et al., 2009). It may also be necessary to examine wood chemical traits in connection with traits associate with the LES (Wright et al., 2004), if we were to fully understand whole-tree economics among co-occurring tree species across highly diverse tropical forests.

The present study focused on Sabah, Malaysia, however, further sites are needed across the tropics, for example, within the Global Ecosystem Monitoring (GEM) network (Malhi et al., 2021) using a standardised protocol. As early nutrient studies suggest that tropical forests should not be categorised as a single entity (Vitousek and Sanford, 1986, Proctor, 1987), the spatial heterogeneity of wood nutrient status is expected across the tropics.

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SUPPORTING INFORMATION

Table S4.1. Mean ratio (± 1 standard error) between nutrient and carbon concentrations in coarse roots (CR), sap wood of trunk bottom (TB), sap wood of trunk middle (TM), branch bottom (BB), and branch middle (BM) (see Fig. 4.1). The values in bold indicated significant differences ($p<0.05$), tested using linear mixed-effects models with the Tukey HSD post-hoc test. The p-values were Bonferroni corrected to account for multiple comparisons.

	N	P	K	Ca	Mg	C
BB wood : BM wood	1.23±0.23	**1.56±0.27**	0.83±0.15	1.32±0.39	0.83±0.19	0.99±0.005
BB wood : CR wood	**1.40±0.18**	**1.88±0.30**	0.95±0.19	1.31±0.37	0.93±0.25	**0.99±0.004**
BB wood : TB sapwood	**2.45±0.34**	**2.52±0.58**	1.35±0.22	1.65±0.42	1.15±0.29	**0.98±0.004**
BB wood : TM sapwood	**1.82±0.26**	**1.71±0.28**	1.19±0.19	1.88±0.50	1.32±0.34	**0.99±0.004**
BM wood : CR wood	1.14±0.19	1.21±0.18	1.14±0.21	1.00±0.25	1.12±0.29	0.99±0.005
BM wood : TB sapwood	**2.00±0.35**	1.61±0.37	1.63±0.24	1.26±0.28	1.38±0.33	**0.99±0.004**
BM wood : TM sapwood	1.49±0.27	1.10±0.18	1.44±0.20	1.43±0.34	1.59±0.39	0.99±0.004
CR wood : TB sapwood	**1.75±0.20**	1.34±0.29	1.42±0.24	1.26±0.26	1.23±0.35	1.00±0.004

CR wood : TM sapwood	1.30±0.15	0.91±0.13	1.26±0.20	1.44±0.32	1.42±0.41	1.00±0.004

Note: Heartwood was not compared with branch and coarse wood components, because these woody tissues are assumed to be mostly sapwood.

Table S4.2. Mean ratio (± 1 standard error) between nutrient and carbon concentrations in bark at branch bottom (BB), branch middle (BM) bark of coarse roots (CR), trunk bottom (TB), and trunk middle (TM) (see Fig. 4.1). The values in bold indicated significant differences ($p<0.05$), tested using linear mixed-effects models with the Tukey HSD post-hoc test. The p-values were Bonferroni corrected to account for multiple comparisons.

	N	**P**	**K**	**Ca**	**Mg**	**C**
BB bark : BM bark	1.01±0.09	1.04±015	0.98±0.13	**1.53±0.27**	1.09±0.26	0.98±0.01
BB bark : CR bark	0.95±0.15	**1.35±0.15**	**1.52±0.19**	1.33±0.21	1.37±0.27	0.99±0.01
BB bark : TB bark	0.85±0.07	**1.84±0.27**	**1.31±0.17**	1.02±0.15	1.30±0.25	1.00±0.01
BB bark : TM bark	0.87±0.07	**1.36±0.18**	1.15±0.15	1.30±0.20	1.29±0.25	0.98±0.01
BM bark : CR bark	0.94±0.15	**1.30±0.16**	**1.55±0.20**	0.87±0.14	1.26±0.28	1.01±0.01
BM bark : TB bark	0.84±0.07	**1.76±0.27**	**1.33±0.17**	**0.66±0.10**	1.19±0.26	1.01±0.01

BM bark : TM bark	0.86±0.07	**1.30±0.19**	1.17±0.16	0.85±0.13	1.18±0.25	1.00±0.01
CR bark : TB bark	0.89±0.14	**1.36±0.18**	0.86±0.11	0.76±0.10	0.95±0.16	1.00±0.01
CR bark : TM bark	0.92±0.14	1.01±0.12	**0.76±0.10**	0.98±0.13	0.94±0.15	0.99±0.01
TB bark : TM bark	1.03±0.08	**0.74±0.11**	0.88±0.11	1.28±0.16	0.99±0.16	0.99±0.01

Table S4.3. Mean concentrations (± 1 SE) of nutrients of N, P, K, Ca, Mg and carbon (C) in bark, sapwood, and heart wood, and wood resorption (%) at the bottom of the trunk (TB), mean for species groups (Dipterocarps, Other non-pioneers, Pioneers) and by species (10 species with three replicates). For the species code, see Table 4.1 in the main text. Resorption (Eq. 1) values are positive when there is nutrient resorption to from heartwood sapwood, while negative values indicate accumulation to heartwood.

Species code	N (%)	P (mg/g)	K (mg/g)	Ca (mg/g)	Mg (mg/g)	C (%)
			Bark			
Dipterocarps mean	0.28±0.02	0.10±0.01	2.35±0.26	15.48±1.50	0.89±0.11	43.60±0.36
DP.m	0.34±0.01	0.14±0.002	3.84±0.23	14.95±0.70	0.85±0.37	44.85±0.19
DS.j	0.24±0.03	0.09±0.02	2.39±0.76	10.18±0.85	1.22±0.11	43.07±0.90
DS.l	0.22±0.03	0.08±0.01	1.97±0.12	17.26±1.97	0.78±0.06	43.96±0.81
DS.m	0.38±0.05	0.10±0.01	1.50±0.16	23.44±2.97	0.40±0.07	42.24±0.77
DS.p	0.23±0.01	0.09±0.02	2.05±0.43	11.57±3.19	1.21±0.06	43.91±0.76
Other non-pioneers mean	0.40±0.07	0.11±0.02	4.06±0.44	9.95±1.84	1.16±0.26	44.97±0.30

FL.l	0.28±0.05	0.08±0.03	3.32±0.63	8.03±1.06	1.70±0.18	45.05±0.42
MP.l	0.53±0.05	0.15±0.02	4.79±0.12	11.88±3.49	0.63±0.14	44.88±0.52
Pioneers mean	0.35±0.01	0.26±0.03	5.34±0.43	15.83±3.07	1.83±0.32	43.49±0.48
CT.o	0.34±0.02	0.20±0.01	5.41±0.36	24.38±2.10	1.67±0.14	43.21±0.33
EM.p	0.36±0.03	0.26±0.07	4.05±0.28	18.80±1.03	2.76±0.64	42.13±0.53
RN.c	0.36±0.02	0.31±0.07	6.55±0.68	4.31±0.61	1.05±0.11	45.11±0.27
			Sapwood			
Dipterocarps mean	0.04±0.003	0.05±0.01	0.910.12	1.68±0.22	0.14±0.01	46.19±0.21
DP.m	0.04±0.01	0.06±0.03	1.50±0.31	1.41±0.16	0.14±0.04	46.19±0.14
DS.j	0.04±0.01	0.05±0.02	0.73±0.32	1.05±0.11	0.16±0.03	46.42±0.31
DS.l	0.04±0.002	0.06±0.005	1.14±0.07	1.45±0.19	0.11±0.04	46.68±0.23
DS.m	0.03±0.01	0.03±0.005	0.46±0.03	3.16±0.50	0.11±0.01	44.83±0.09
DS.p	0.03±0.01	0.04±0.01	0.74±0.09	1.33±0.07	0.19±0.03	46.81±0.31

Other non-pioneers mean	0.06±0.01	0.04±0.01	1.53±0.12	0.97±0.22	0.36±0.01	46.20±0.21
FL.l	0.04±0.004	0.02±0.003	1.29±0.22	0.91±0.16	0.35±0.05	46.18±0.21
MP.l	0.08±0.02	0.05±0.01	1.77±0.31	1.02±0.39	0.37±0.07	46.23±0.02
Pioneers mean	0.03±0.01	0.11±0.01	1.73±0.20	0.78±0.19	0.67±0.04	45.70±0.10
CT.o	0.03±0.003	0.04±0.01	1.55±0.10	0.97±0.15	0.17±0.02	45.37±0.23
EM.p	0.04±0.004	0.17±0.10	1.91±0.40	0.59±0.12	1.18±0.06	46.03±0.19
RN.c	0.07±0.01	0.13±0.02	2.15±0.44	0.52±0.03	0.21±0.02	45.21±0.11

Heartwood

Dipterocarps mean	0.03±0.002	0.01±0.003	0.45±0.19	2.27±0.22	0.31±0.03	46.26±0.28
DP.m	0.03±0.004	0.03±0.005	1.65±0.54	3.51±0.27	0.32±0.11	45.70±0.33
DS.j	0.03±0.003	0.00±0.002	0.07±0.03	1.88±0.37	0.33±0.08	46.93±0.02
DS.l	0.02±0.001	0.01±0.001	0.33±0.13	1.92±0.06	0.26±0.02	46.80±0.09
DS.m	0.02±0.003	0.01±0.003	0.13±0.06	2.72±0.12	0.23±0.01	44.58±0.37

DS.p	0.02±0.002	0.01±0.01	0.07±0.01	1.35±0.09	0.40±0.03	47.31±0.27
Other non-pioneers mean	0.07±0.01	0.04±0.01	1.83±0.25	1.56±0.35	0.49±0.03	45.57±0.12
FL.l	0.04±0.001	0.03±0.004	1.92±0.30	1.37±0.37	0.47±0.05	45.56±0.07
MP.l	0.09±0.02	0.05±0.01	1.74±0.46	1.75±0.67	0.52±0.03	45.59±0.26
Pioneers mean	0.06±0.01	0.10±0.01	3.15±0.81	3.06±0.99	1.07±0.38	44.92±0.17
CT.o	0.05±0.01	0.06±0.02	5.33±1.87	2.90±0.60	0.35±0.07	44.52±0.27
EM.p	0.05±0.01	0.11±0.03	1.30±0.18	5.62±2.28	2.51±0.38	44.85±0.20
RN.c	0.09±0.01	0.12±0.003	2.81±0.50	0.65±0.03	0.34±0.04	45.40±0.18

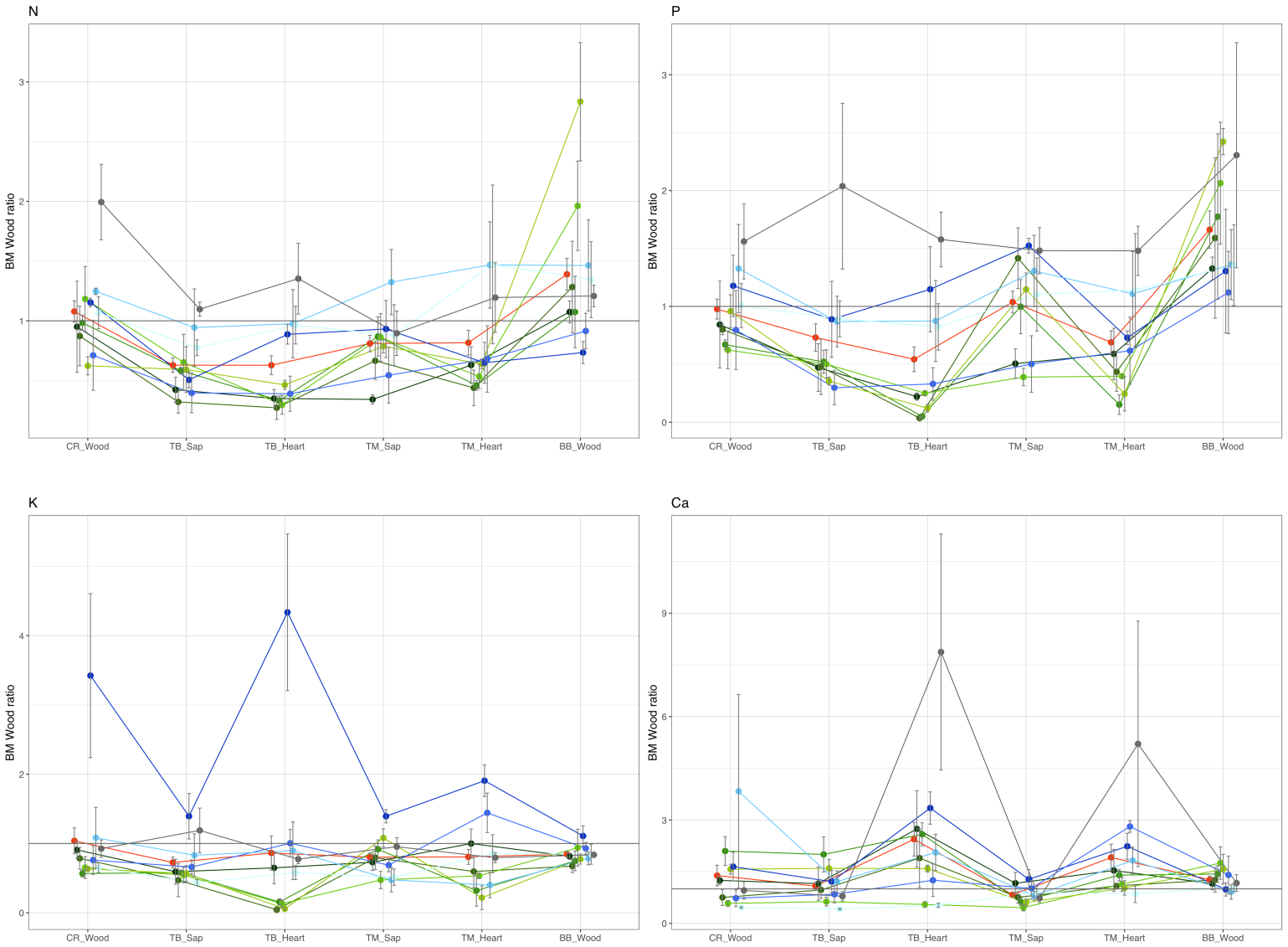
Species code	**N (%)**	**P (%)**	**K (%)**	**Ca (%)**	**Mg (%)**	**C (%)**
			Wood resorption			
Dipterocarps mean	25.3±3.6	60.3±14.4	56.2±11.5	-53.5±5.7	-139.9±21.4	-0.2±0.003
DP.m	14.8±3.2	14.4±7.4	-4.1±1.6	-152.5±20.8	-166.4±75.8	1.1±0.01
DS.j	11.8±3.7	96.6±61.6	51.6±30.9	-85.2±19.0	-123.6±36.7	-1.1±0.01

DS.l	43.3±3.2	90.2±14.7	72.0±29.5	-38.1±5.2	-167.6±60.2	-0.3±0.001
DS.m	48.9±16.9	45.5±11.9	71.3±32.2	10.6±1.7	-120.3±12.6	0.6±0.005
DS.p	7.6±1.9	67.0±31.2	90.3±20.4	-2.3±0.2	-121.8±24.3	-1.1±0.01
Other non-pioneers mean	-8.8±2.1	-12.3±2.2	-23.2±5.9	-59.7±20.7	-49.2±6.9	1.4±0.01
FL.l	-6.7±0.7	-16.9±3.5	-50.5±11.8	-48.0±15.4	-40.8±7.4	1.3±0.01
MP.l	-11.0±4.0	-7.6±2.7	4.1±1.3	-71.4±38.4	-57.5±11.5	1.4±0.01
Pioneers mean	-46.0±7.8	-15.0±5.9	-90.4±31.2	-366.6±129.5	-100.7±11.5	1.3±0.01
CT.o	-88.0±22.4	-48.8±17.4	-261.8±93.1	-221.3±58.0	-123.0±27.7	1.9±0.01
EM.p	-21.5±3.3	-3.4±2.3	22.6±5.7	-852.6±384.1	-113.1±18.1	2.6±0.02
RN.c	-28.7±5.8	7.3±1.2	-31.9±-8.7	-25.8±2.2	-66.1±9.6	-0.4±0.002

Table S4.4. Soil characteristics of the study site. Concentrations of total C, N, P, K Ca, Mg, effective cation exchange capacity (eCEC), pH (H_2O), and sand:clay ratio by soil layer depth to 300 cm **in the SAFE Project SAF-03** (about 1.5 km from where woody samples were collected)**.**

Depth (cm)	**C (%)**	**N (%)**	**P (mg/kg)**	**K (mg/kg)**	**Ca (mg/kg)**	**Mg (mg/kg)**	**eCEC (mmol+/kg)**	**pH**	**Sand:Clay**

0-5	0.355	0.094	173.28	56.99	133.01	38.08	22.14	4.00	26.07
5-10	0.288	0.094	133.38	37.09	18.96	12.77	20.64	4.07	4.47
10-20	0.236	0.095	106.21	34.04	22.45	13.64	28.86	4.01	6.39
20-30	0.440	0.096	94.57	22.67	6.17	6.76	20.92	4.35	6.64
30-50	0.644	0.099	68.96	27.01	7.44	8.22	19.69	4.78	6.05
50-100	0.202	0.100	75.84	31.45	5.80	10.70	25.31	4.56	5.50
100-150	0.149	0.103	73.26	46.58	4.65	7.48	32.40	4.60	4.74
150-200	0.677	0.107	75.78	48.07	5.96	6.96	29.63	4.57	6.58
200-250	0.408	0.108	77.44	67.88	57.26	21.06	25.69	5.18	12.17
250-300	0.529	0.110	75.35	62.41	12.37	13.59	27.52	4.76	7.63


N
P
K
Ca
BM Wood ratio
CR_Wood
TB_Sap
TB_Heart
TM_Sap
TM_Heart
BB_Wood

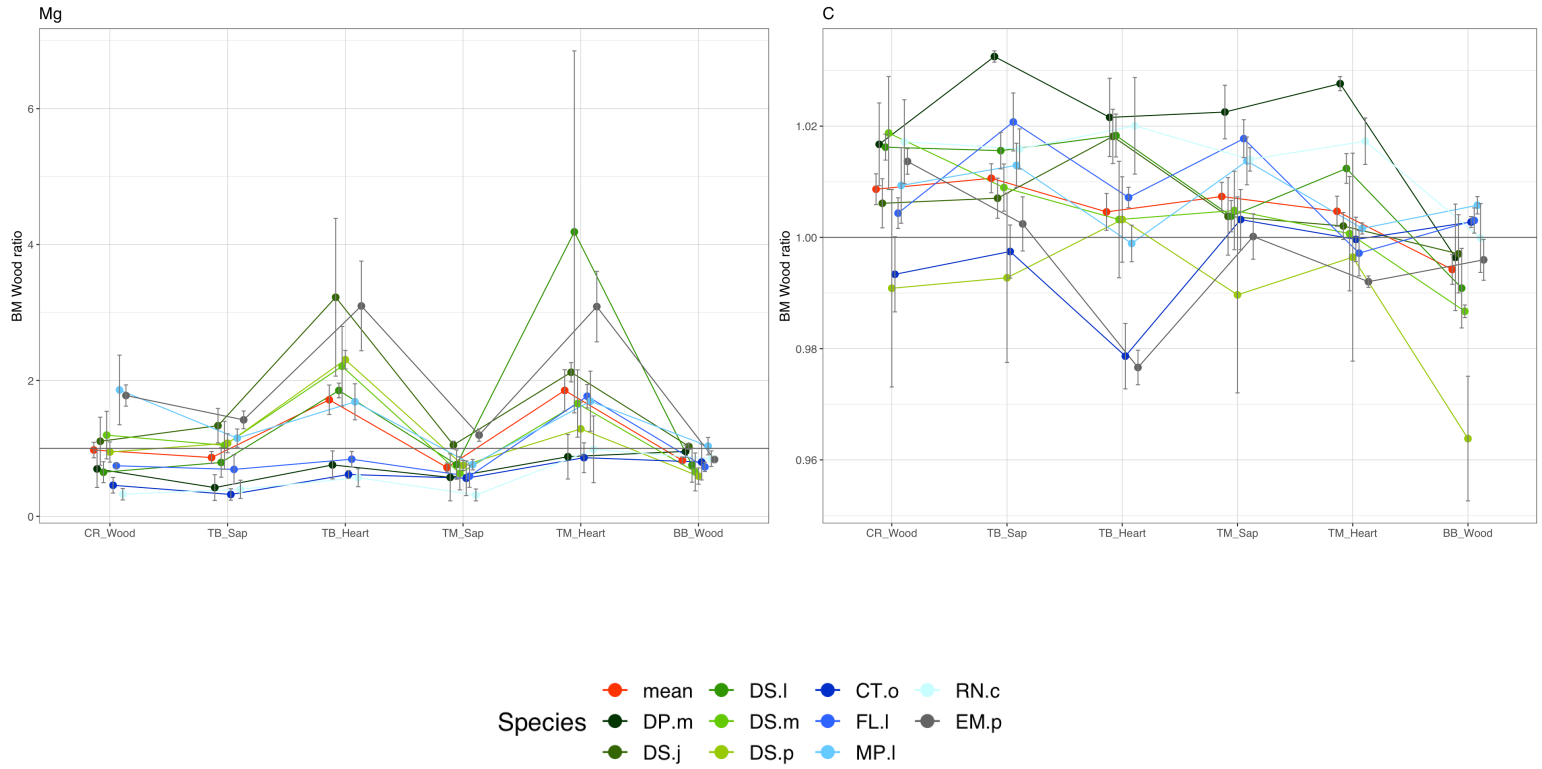
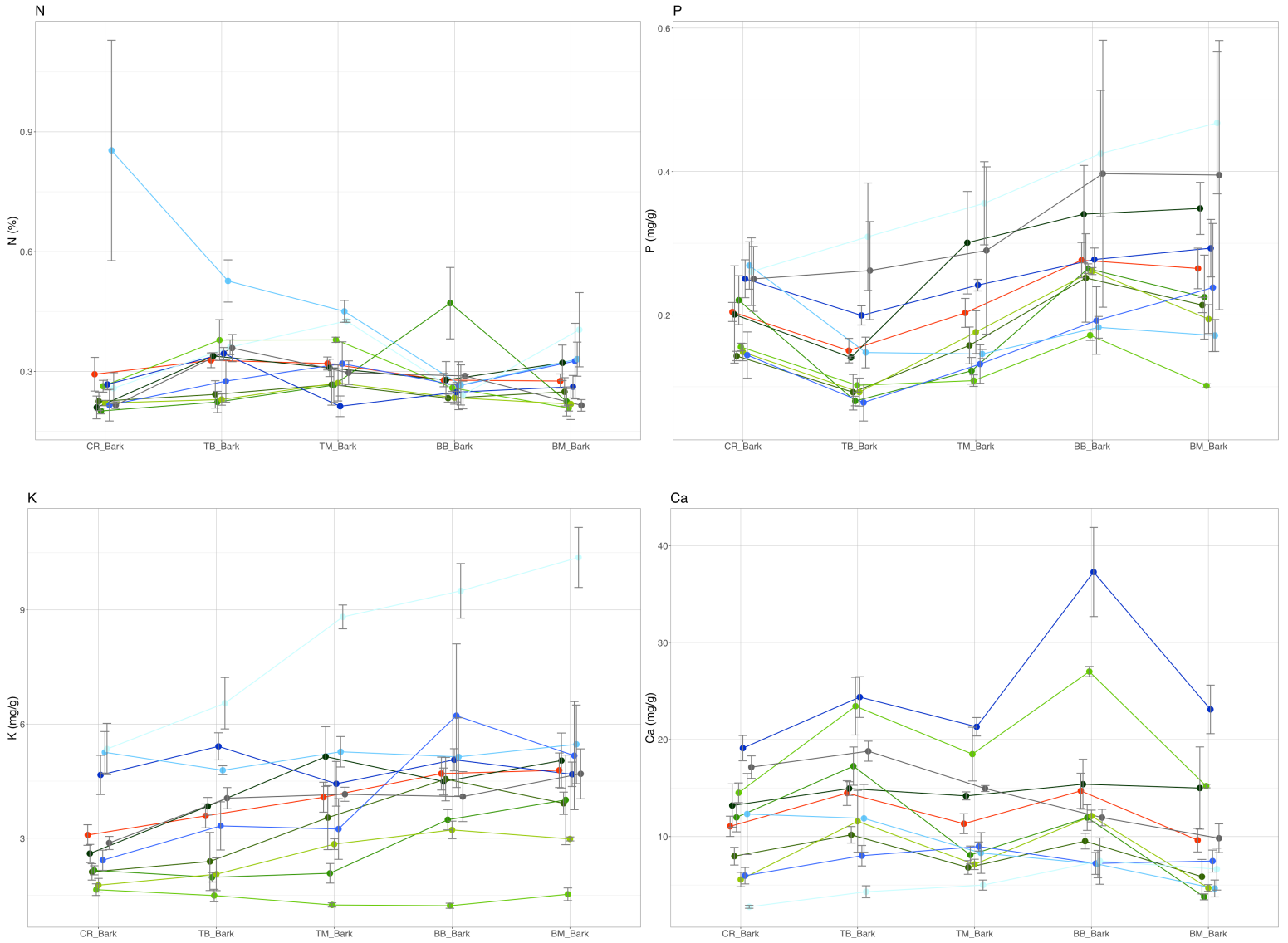


Figure S4.1. Nutrient and carbon concentrations in woody components relative to wood in branch middle (BM) (in ratio) along the length of the tree.

Woody components on x-axis are coarse root (CR) wood, trunk bottom (TB) sapwood, trunk bottom (TB) sapwood, trunk middle (TM) sapwood, trunk middle (TM) heartwood, and branch bottom (BB) wood (see Fig. 4.1 and 4.2). Values (±SE) were averaged per species (*n* = 3). Red line indicates total mean, and other coloured lines indicate mean of each species (see Table 4.1). Note the different scales of the y axes.


N
N (%)
0.9
0.6
0.3
CR_Bark
TB_Bark
TM_Bark
BB_Bark
BM_Bark
P
P (mg/g)
0.6
0.4
0.2
CR_Bark
TB_Bark
TM_Bark
BB_Bark
BM_Bark
K
K (mg/g)
9
6
3
CR_Bark
TB_Bark
TM_Bark
BB_Bark
BM_Bark
Ca
Ca (mg/g)
40
30
20
10
CR_Bark
TB_Bark
TM_Bark
BB_Bark
BM_Bark

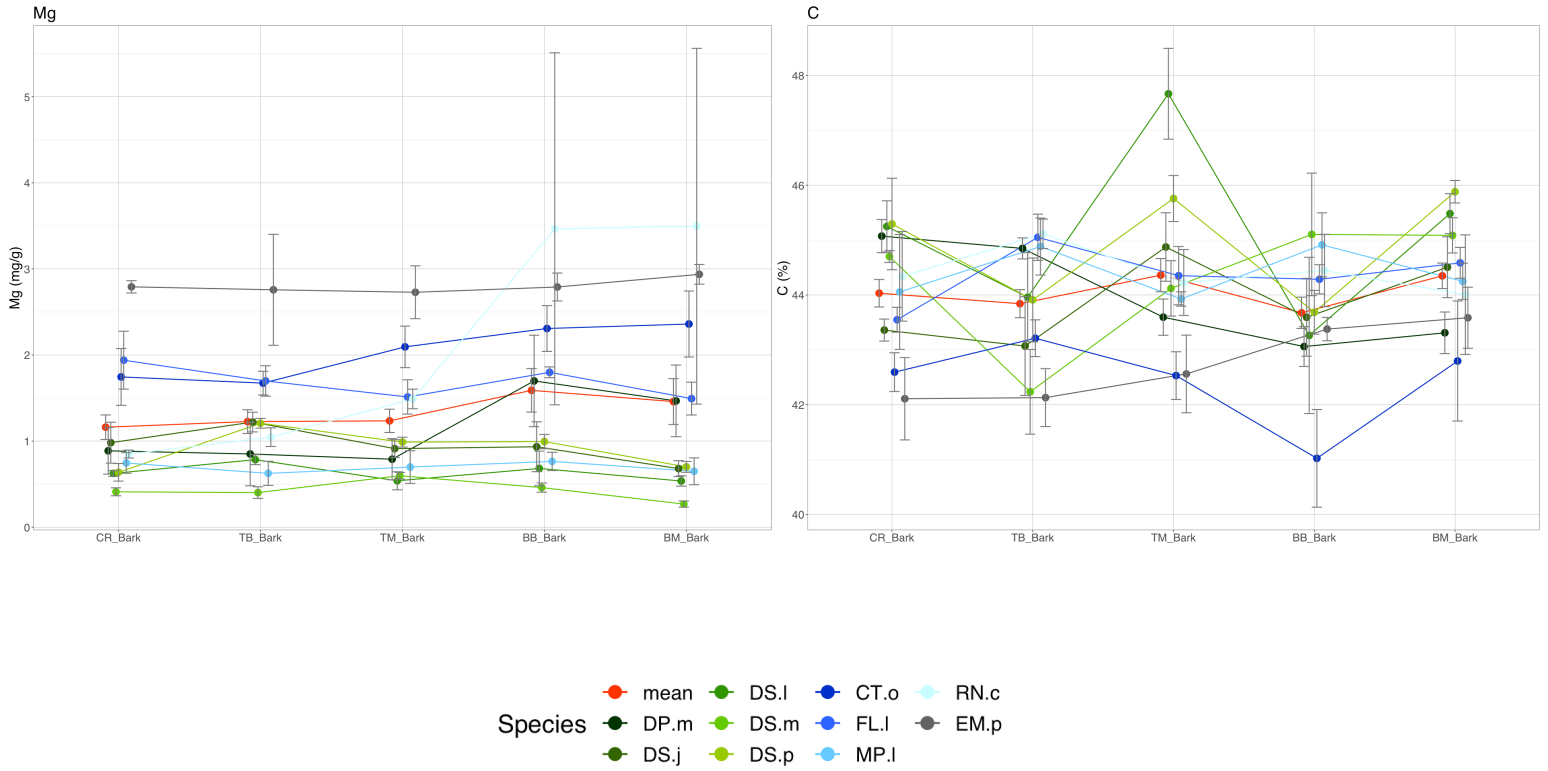
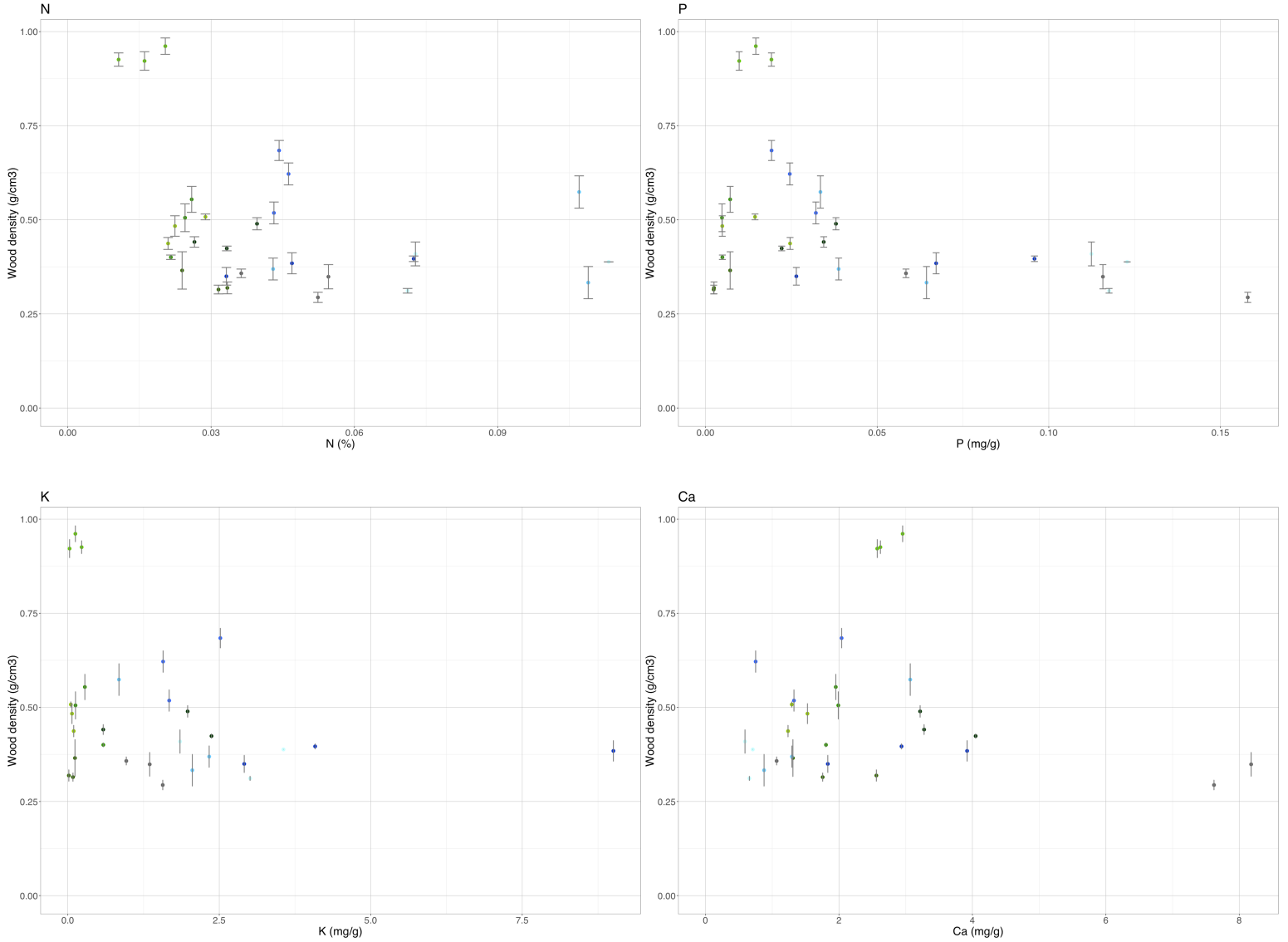


Figure S4.2. Nutrient and carbon concentrations in bark along the length of the tree. The components on x axis are coarse root (CR), trunk bottom (TB), trunk middle (TM), branch bottom (BB), and branch middle (BM) (see Fig. 4.1 and 4.2). Values are mean (±SE) of each species (*n* = 3) (see Table 4.1), and the red line indicates total mean across species. Note the different scales of the y axes.


N
P
K
Ca
Wood density (g/cm3)
N (%)
P (mg/g)
K (mg/g)
Ca (mg/g)
1.00
0.75
0.50
0.25
0.00
0.00
0.03
0.06
0.09
0.05
0.10
0.15
0.0
2.5
5.0
7.5
0
2
4
6
8

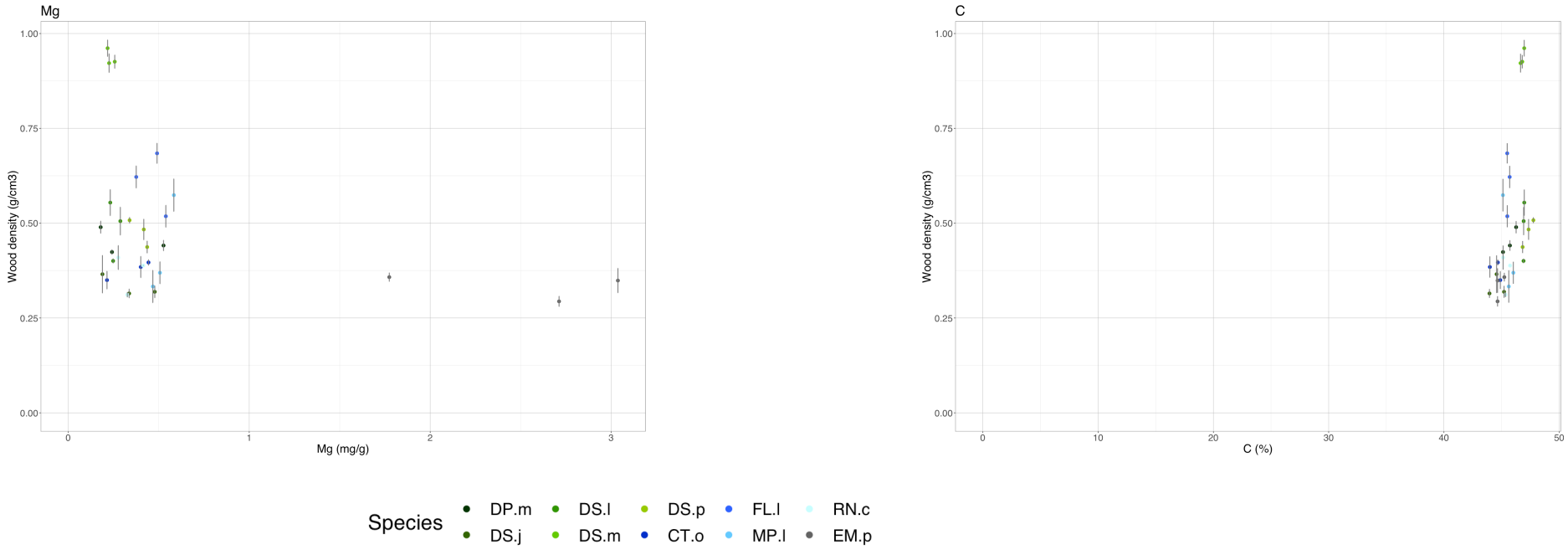


Figure S4.3. Correlation between wood nutrient and carbon concentrations, and wood density in trunk bottom (TB). We sampled ten species (grouped into dipterocarps, other non-pioneers and pioneers) with three replicate trees. Species codes are listed in Table 4.1. Each data point is the mean (±SE) of an individual tree with two to five samples taken per tree. The correlation between the nutrient concentration and wood density was not significant for any of the nutrients (Pearson's correlation coefficient was 0.0523 for Calcium and >0.1 for all other nutrients).

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Chapter 5, Overview

In the previous chapter, I studied individual trees. In this chapter, I move to whole ecosystem nutrient budgets. I use a novel approach of combining estimates of net primary productivity with nutrient stoichiometry. I am thus able to quantify (i) nutrient requirement of the ecosystem, partitioned into canopy, woody and fine root requirement, (ii) leaf resorption rates and the contribution of resorption towards meeting the nutrient requirement, (iii) nutrient uptake rates from the soil and (iv) nutrient use efficiency. I compare the nutrient budgets across a logging disturbance gradient, ranging from heavily, moderately and lightly logged forests to intact old-growth forests in Malaysian Borneo. To my best knowledge, this is the first attempt at coupling NPP and stoichiometry in tropical forests.

I conceived the study together with my supervisors and led on the analyses and writing. I collected all the data on the nutrient stoichiometry. Terhi Riutta and Kho Lip Khoon collected the net primary productivity data. Noreen Majalap-Lee led the chemical analyses. Reuben Nilus helped with the species identification and fieldwork logistics.

Chapter 5 Nutrient uptake, use efficiency, resorption and allocation along a disturbance gradient in Bornean tropical forests

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Abstract

Nutrients such as nitrogen (N) and phosphorus (P) are likely to play important roles in determining the productivity and carbon cycling in most ecosystems. However, there have been very few direct studies of nutrient uptake and nutrient use efficiencies in tropical forests, amongst the most productive of ecosystems, because such studies require not only the measurement of nutrient stoichiometry and stocks but also net primary productivity (NPP). Here we report the rates of nutrient uptake and nutrient use efficiencies in nine intensive carbon plots along a logging disturbance gradient in Malaysian Borneo, as well as nutrient resorption by green leaves and the resorption

contribution to total and canopy nutrient requirement. We report values for the whole forest stand and also partitioned into canopy, wood and fine roots.

While there was substantial site-to-site variation in the pattern of nutrient uptake and nutrient use efficiency, some broad patterns emerged. A large fraction of nutrient uptake, ranging from 58.9% (N) to 46.8% (calcium [Ca]), was allocated to the canopy in old-growth forests, whereas it was more evenly allocated to both the canopy and woody components in logged forests. Nutrient allocation to fine roots appeared relatively invariant across plots. In old-growth forests, nutrient resorption contributed more to meeting total nutrient requirement than in logged forest. In old-growth forests, resorption provided 34.6±2.4% (N), 44.5±6.4% (P), 45.7±4.5% (potassium [K]), and 15.6±1.6% (magnesium [Mg]) of the nutrient requirement, while in logged forest the corresponding values were 27.3±2.2% (N), 35.7±2.3% (P), 21.7±1.8% (K) and 2.5±2.3% (Mg), respectively.

On the other hand, there was no strong pattern in nutrient resorption rate, nutrient requirement, nutrient uptake or nutrient use efficiency related to the logging disturbance, except for K, which had lower resorption rate and higher uptake in the more disturbed sites. Nitrogen use efficiency and resorption appeared less variable across sites than other elements, suggesting that N supply is not constrained at any of the sites. Overall, this study demonstrates the value of coupling NPP with stochiometric data to gain insights into the nutrient cycle of intact and disturbed forests.

Key words: carbon cycling; ecophysiology; Malaysian Borneo; net primary productivity; NPP; nutrient

cycling; nutrient uptake; nutrient resorption; tropical forest

INTRODUCTION

Tropical forests only cover about 10% of Earth's land surface, but they account for 34% of terrestrial net primary production (NPP) and hold about 25% of the terrestrial biomass carbon (C) (Lewis et al., 2009, Malhi, 2012). They are also estimated to account for nearly 70% of terrestrial nitrogen (N) fixation, and are responsible for nearly 50% of terrestrial nitrous oxide (N_2O) emissions (Wang and Houlton, 2009).

Nutrients such as N and phosphorus (P) are likely to play important roles in determining the magnitude of C cycling in tropical forests both individually and in combination (Chave et al., 2010, Vitousek et al., 2010). Nitrogen-rich enzymes regulate photosynthetic CO_2 fixation (Field and Mooney, 1986, Reich et al., 1997), and P-rich RNA and ATP determine cellular biosynthesis (Sterner and Elser, 2003). In addition, base cations such as potassium (K), calcium (Ca), and magnesium (Mg) are essential for plant metabolism and physiological processes related to growth (Likens and Bormann, 1995, Fromm, 2010). While most coupled C cycle-climate models presume that only C inputs via photosynthesis constrain NPP and C sequestration, a recent global synthesis concludes that nutrient availability is the key regulator of forest C balance and sequestration (Fernández-Martínez et al., 2014). It is therefore important to account for nutrient-C interactions to avoid substantial errors in predicting

how tropical ecosystems respond to increasing atmospheric CO_2, climate change and disturbance (Townsend et al., 2011, Malhi, 2012).

Nutrient uptake is one of key indicators for nutrient-C interactions, because it potentially constrains NPP (Vitousek and Howarth, 1991, Elser et al., 2007). Nutrient uptake is the amount of nutrients accrued from the soil for plant growth, and can be quantified by combining estimates for NPP and nutrient stoichiometry (in this case, the ratio of each nutrient to C) of live and senesced tissue. To our knowledge, however, there has been no direct attempt at coupling NPP with nutrient stoichiometry to estimate nutrient uptake in tropical forests, because a complete estimation of NPP in large-stature tropical forests is challenging (Clark et al., 2001) and until recently has been relatively uncommon. It is also poorly known how nutrient uptake and concentrations are allocated to tree organs such as green leaves, branches and fine roots. Nutrient allocation among such organs constrains plant growth and life-history strategies (Grime, 2001, Kerkhoff et al., 2006), and allocation patterns by plants may vary between N and P limited conditions (Aoyagi and Kitayama, 2016). Unlike C and N, which have been quantified elsewhere (Millard and Grelet, 2010), direct measurements of P concentrations and stocks in wood (Feldpausch et al., 2004, Heineman et al., 2016, Johnson et al., 2001) and fine roots (Li et al., 2010) are scarce in tropical forests, particularly in Southeast Asia (e.g., Aoyagi and Kitayama, 2016). In contrast, soil and leaf P concentrations and stocks are well documented across the tropics (Wright et al., 2005, Hidaka and Kitayama, 2009).

Plants on less fertile soils tend to use nutrients more efficiently as indicated by less nutrient return via litterfall to soil (Silver, 1994). Nutrient use efficiency is estimated as the ratio of biomass increment to nutrient requirement (Hirose, 1975), i.e. total NPP per unit of nutrient usage (Bridgham et al., 1995) and largely reflects the mean stoichiometry of the living biomass weighted according to the productivity of each organ. It can be measured at leaf, plant or ecosystem scale (Grubb, 1989, Ewel and Hiremath, 1998). Previous studies in tropical forests have focused either on the nutrient use efficiency of fine litter production (Silver, 1994, Kitayama et al., 2000) or photosynthetic leaves (Hidaka and Kitayama, 2013), but comprehensive studies of whole-forest nutrient use efficiency are scarce (e.g., Hiremath et al., 2002, Paoli et al., 2005). Nutrient use efficiency is also a key concept for understanding how resource availability determines spatial patterns of NPP (Chapin, 1980, Vitousek, 1982). For example, high phosphorus use efficiency may indicate P limitation to N:P ratio: in other words, less P efficient forests can be expected to be found on P-rich soils (Vitousek, 1982, Silver, 1994).

About 50% of foliar N, P and K is resorbed by plants from leaves during leaf senescence (Yuan and Chen, 2009, Chapin et al., 2011). A meta-analysis by McGroddy et al. (2004) reports that P resorption is greater relative to N and C in tropical forests, while data is especially limited for base cations (Kazakou et al., 2007, Yuan and Chen, 2009). Leaf mass loss should also be taken into account for the unbiased estimation as leaf mass changes during senescence (van Heerwaarden et al., 2003, Kazakou et al., 2007), mainly due to the resorption of C and nutrients

followed by leaching and *in situ* decomposition (Vergutz et al., 2012). Improved understanding of nutrient resorption and how and why they vary are imperative for predicting long-term NPP and nutrient cycling (Thornton et al., 2007, Chapin et al., 2011). Furthermore, it is not known what fraction of the nutrient requirement can be met through resorption, and how much this varies among nutrients.

The area of logged and human-modified forests tropical forests now exceeds that of old-growth forests (Potapov et al., 2008, FAO, 2015), making it imperative to understand nutrient dynamics in logged forests. Logging removes nutrients as timber, and logging operations and the release of a large quantity of nutrients from necromass lead to the erosion and leaching of soil nutrients (Steege et al., 1996). Furthermore, logging may have a significant effect on the nutrient cycling of the remaining stand due to changes in forest structure, species composition and microclimate. The effect of logging on nutrient budgets is related to logging intensity (Bruijnzeel and Proctor, 1995), logging rotation period, tree species composition, rainfall patterns, and soil properties (Kobayashi, 1994). In Malaysian Borneo, Imai et al. (2012a) documented that exported amounts of C, N and P increased linearly with increasing logging intensity, and heavy selective logging would induce P-limitation in the following regrowth period. Calcium deficiency is also documented after logging in Sabah (Nykvist, 1997, 1998, 2000). In contrast, a study in the Brazilian Atlantic forest demonstrated that selective logging had no effect on nutrient concentrations and C:N ratio in the soil or in the litter, although leaf litter production and input decreased (Villela et al., 2006). In the eastern Amazon, deforestation caused a temporary shift from P

limitation in old-growth forests, to N limitation in converted pastures and early successional forests, and to increasing P constraints when forests became mature again (Davidson et al., 2007). This can be explained by the fact that forest conversion induces greater N losses relative to those of P, and then N fixation restores N stocks over long-term (Townsend et al., 2011). Proctor (1995) argues that moderate logging would not cause significant nutrient limitation because the factors contributing to soil erosion, eluviation and leaching are limited.

These inconsistent findings across the tropics underscores the need for a better understanding of the logging impacts on nutrient dynamics in disturbed forests in comparison with undisturbed forests. The aim of this study is, therefore, to quantify key biological processes of nutrient cycling (resorption rates, use efficiency, uptake, uptake efficiencies, and allocation) along a disturbance gradient from heavily and moderately logged to old-growth forests in Malaysian Borneo. As a recent global synthesis on nutrient resorption identifies that no datasets exist in Southeast Asia except two sites in northern Thailand (Vergutz et al., 2012), our study provides the first resorption estimates including K, Ca and Mg in Borneo. To our knowledge, it is also the first attempt at coupling NPP and nutrient stoichiometry to quantify nutrient uptake and use efficiencies of five macronutrients in tropical forests. This study takes a plant community-level approach (in this case, plot-level) to estimate nutrient requirement, uptake, use efficiency, uptake efficiency, resorption and allocation. We address the following research questions:

Q1) What are the rates of leaf nutrient resorption, and how do they vary along a logging

disturbance gradient and among plots, and how much do they contribute to plant nutrient requirement? We expect that old-growth forests will show a tighter nutrient cycle (higher resorption) for most nutrients, but a lower resorption for N.

Q2) How do nutrient requirement, nutrient uptake and nutrient use efficiency vary along a logging disturbance gradient? We expect more disturbed forests will have higher nutrient demands overall, but the P will have a tighter nutrient cycle (high P use efficiency and resorption) in old-growth forests and N with have a tighter cycle (high N use efficiency and resorption) in logged forests.

Q3) How does the requirement for nutrients vary among organs (leaf, wood and fine root) in ecosystems, and how is the total requirement and soil uptake for new nutrients partitioned between organs? We expect the canopy leaves to exert the highest overall demand for nutrients, because of their high physiological activity, even after resorption is accounted for.

MATERIALS AND METHODS

Plot descriptions:

The study was conducted in nine permanent intensive carbon plots located across the states of Sabah and Sarawak, Malaysian Borneo (Table 5.1). The plots are part of the Global Ecosystems Monitoring (GEM) network (see

http://gem.tropicalforests.ox.ac.uk; Malhi et al., 2021). The vegetation type is a mixed dipterocarp lowland rainforest, which is the most extensive forest type in Malaysian Borneo. Five plots, located in Kalabakan Forest Reserve, Sabah, had been previously logged at different intensities (Ewers et al., 2011, Struebig et al., 2013), constituting a disturbance gradient from heavily to moderately logged forest plots (Riutta et al., 2018). Two old-growth forest plots were located in Maliau Basin Conservation Area, Tongot District, Sabah, and the other two in Lambir Hills National Park, Miri District, Sarawak. Neither old-growth forest area had any record of either logging or other structural disturbance. The Sabah plots are part of the Stability of Altered Forest Ecosystems (SAFE) Project, one of the world's largest experiments in human-modified forest landscapes (Ewers et al., 2011). All nine plots had a planimetric area of 1 ha, which was divided into 25 subplots of 20 m × 20 m. A description of all the plots and their productivity is given in Riutta et al. (2018).

The study plots in Sarawak harbour the highest recorded tree species richness in the Paleotropics (Palmiotto et al., 2004, Ashton, 2005). In all plots, Euphorbiaceae and Dipterocarpaceae were the most species-rich families among trees >10 cm DBH, with the Dipterocarpaceae dominating in overall biomass. In the old-growth plots, the most common genera were the dipterocarp genera *Shorea* and *Parashorea* in Maliau, *Shorea* and *Dryobalanops* in Lambir, while in the logged plots the most common genera were *Macaranga* (Euphorbiaceae), *Shorea* (Diptocarpaceae) and *Syzygium* (Myrtaceae). See Kho et al. (2013), Riutta et al. (2018), and Both et al. (2019) for detailed description of the species composition.

Soils around the study plots in Sabah have developed over rocks of the Kuamut formation and are mainly orthic Acrisol or Ultisols, formulated on sandstone and mudstone (Burghouts, 1993). In the study plots in Sarawak, soils vary between sandstone-derived sandy loam humult Ultisols on ridges, and shale-derived clay of clay-rich udult Ultisols (Kho et al., 2013) in valleys. For soil nutrient contents see Table 5.2. The mean annual temperature and precipitation in the region are 26.7 ±1.9 °C and 2600-2700 mm (Walsh and Newbery, 1999, Kumagai et al., 2004, Kumagai and Porporato, 2012). Although no distinct seasonality exists in typical years, some drier months occur in most years, and ecologically significant droughts occur during El Niño events (Malhi and Wright, 2004). As there is no regular dry season at any of these sites, this study controls for the effect of water stress on NPP, enabling us to isolate soil nutrient controls on NPP and nutrient cycling separate from water stress factors.

The short distance (typically a few km) between some plots could potentially raise issues of pseudoreplication (Malhi et al., 2015). However, the two adjacent plots both in Maliau and Lambir sites showed considerable differences in soil conditions and species composition, sufficient to treat them as independent sample points. In Lambir, one plot is on relatively fertile clay soil, while the other is on relatively infertile sandy soil (Table 5.2). Logged plots in close proximity can also be treated as independent due to high spatial heterogeneity in logging intensity. See also multivariate analyses in Riutta et al. (2018) and Both et al. (2019), showing that variation within forest types is larger than between forest types.

Table 5.1 Characteristics of the study plots

Plot code[a]	Plot location	Disturbance	Soil type; topography	Basal area of trees > 10 cm DBH (m^2 ha^{-1})[b]	Mean canopy gap fraction (%)[b]	Mean forest quality score[c]
SAF-01	SAFE Project Experimental Area (4.732°, 117.619°), Sabah	Heavily logged	Clay; mostly flat with a moderate slope on one edge	6.81 ± 1.00	15.0 ± 2.14	2.2
SAF-02	SAFE Project Experimental Area (4.739°, 117.617°), Sabah	Heavily logged	Clay; undulating	11.1 ± 1.81	13.4 ± 1.51	2.6
SAF-05	SAFE Project Experimental Area (4.716°, 117.609°), Sabah	Heavily / moderately logged	Clay; undulating	13.9 ± 1.70	12.2 ± 2.07	2.7
SAF-04	SAFE Project Logged Forest Area (4.765°, 117.700°), Sabah	Moderately logged	Mostly sandy loam, partly clay; flat	19.3 ± 1.70	12.8 ± 1.03	3.2

SAF-03	SAFE Project Experimental Area (4.691°, 117.588°), Sabah	Moderately logged	Clay; steep slope	19.6 ± 1.88	11.2 ± 1.29	3.2
MLA-02	Maliau Basin Conservation Area (4.754°, 116.950°), Sabah	Old-growth	Clay; moderate slope	34.7 ± 2.74	7.04 ± 0.55	5.0
MLA-01	Maliau Basin Conservation Area (4.747°, 117.700°), Sabah	Old-growth	Clay; undulating	41.6 ± 3.59	8.70 ± 0.62	5.0
LAM-07	Lambir Hills National Park (4°12'N, 114°2'E), Sarawak	Old-growth	Clay; undulating valley bottom	31.8 ± 3.85	10.5 ± 0.45	5.0
LAM-06	Lambir Hills National Park (4°12'N, 114°2'E), Sarawak	Old-growth	Sandy loam; undulating ridge top	41.1 ± 2.45	9.52 ± 0.22	5.0

[a]Plot code as in the ForestPlots database (ForestPlots.net)

[b]DBH – Diameter at breast height (1.3 m); Basal area and gap fraction denote the mean ± 1 SE of individual subplots.

[c]Individual 20 m × 20 m subplots within each 1 ha plot (*n* = 25) were subjectively ranked into the forest quality classes *a priori,* from 1 (heavily disturbed) to 5 (no signs of human disturbance), using the presence of stumps and felled trees, evidence of logging trails, number of large (≥ 30 cm DBH) trees and canopy closure as the assessment criteria.

Table 5.2 Soil characteristics of the study plots. Weighted mean (± 1 SE) concentrations of total C, N, P, K Ca, Mg, effective cation exchange capacity (eCEC), pH (H2O), sand and clay ratio by topsoil layer depth to 30 cm.

Plot code	C (%)	N (%)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	eCEC (mmol+/kg)	pH	Sand (%)	Silt (%)	Clay (%)
SAF-01	1.23	0.137	255.6	73.3	403.6	124.4	59.4	4.34	49.5	30.6	20.0
	±0.56	±0.05	±38.7	±9.6	±155.5	±44.8	±3.2	±0.08			
SAF-02	0.63	0.064	115.6	84.3	70.0	42.3	51.1	4.26	44.5	36.0	19.5
	±0.38	±0.03	±4.2	±18.2	±0.90	±15.1	±2.2	±0.19			
SAF-05	1.87	0.196	366.4	49.1	398.0	314.7	54.7	4.85	20.8	51.7	27.5
	±0.33	±0.04	±42.5	±1.4	±134.0	±50.8	±4.8	±0.25			
SAF-04	2.96	0.178	66.5	30.1	35.6	17.6	6.2	4.14	46.2	31.5	22.3

	±0.97	±0.02	±4.5	±7.3	±12.8	±2.9	±1.7	±0.57			
SAF-03	0.98	0.104	150.0	79.6	28.0	20.8	32.7	3.80	65.6	24.9	9.5
	±0.43	±0.01	±20.0	±25.2	±3.4	±25.2	±6.3	±0.18			
MLA-02	1.02	0.126	199.2	67.4	90.4	87.7	46.4	4.26	35.7	44.4	19.9
	±0.22	±0.02	±11.1	±13.6	±34.6	±57.6	±2.3	±0.29			
MLA-01	0.80	0.084	141.4	71.1	22.6	30.6	44.9	3.99	43.5	33.9	22.6
	±0.25	±0.01	±15.8	±7.6	±6.7	±7.47	±7.0	±0.08			
LAM-07	0.95	0.098	126.9	61.9	68.0	89.2	36.0	4.49	45.6	42.7	11.7
	±0.07	±0.02	±NA	±21.3	±5.77	±46.7	±6.9	±0.16			
LAM-06	1.16	0.089	73.4	42.5	4.1	9.2	30.4	4.38	69.1	19.2	11.8
	±0.08	±0.01	±NA	±10.4	±2.2	±4.4	±9.1	±0.03			

Sampling of tree components:

Nutrient samples were collected between January and March in 2014. We selected 15 trees (≥ 10 cm diameter at breast height [DBH]), consisting of five tree species with three replicates each (n = 15) outside, but within 100 m of the plot boundary of each plot, representing the most common species of the plot (see Table S5.1). Sampled trees had no visible damage (e.g. no insect damage, chlorotic leaves, bent stems). Four tree components were collected from each tree: branches, green leaves, senesced leaves and fine roots. The total number of samples was 540 (5 trees species × 3 replicates × 4 components × 9 plots). Collected voucher specimens of chosen trees were identified at the species level at the herbarium of the Forest Research Centre in Sabah, Malaysia.

Mature branches with fully expanded green leaves were obtained using a long pole with a saw blade, by tugging a rope cast over a branch with a fishing rod, or by climbing. Although the collection of sun leaves is often recommended by functional trait protocols for foliar nutrient analysis (Cornelissen et al., 2003), we collected shade leaves because the majority of trees and leaves (≥ 10 cm DBH) were shaded, particularly in old-growth plots. It was also to ensure a consistency in the leaf sampling across plots, and to match green leaves against freshly fallen senesced leaves for leaf resorption estimation assuming that the majority of fallen leaves were shade leaves. The selection of sun and shade leaves is unlikely to be influential. A study of 32 leaf traits across 284 species in Borneo, where the data were collected partly from the

same plots as this study, found no systematic differences between sun and shade leaves (Both et al., 2019). Similarly, an analysis of leaf plasticity to light showed that the species ranking in mean concentrations of N and P was maintained across sun and shade leaves for 38 tropical tree species in Bolivia (Rozendaal et al., 2006). All sampled branches were ≥ 1 cm in diameter and were dissected into disks. The disks were taken in the midpoint of the branch (i.e. not near the trunk nor the tip of the branch). Newly shed senesced leaves were collected from the ground; all such collected leaves were intact, fully brown and identical in shape and size to the green leaves. Twenty green and senesced leaves from each individual tree were collected for chemical analysis, and were pooled, resulting in one sample of green leaves, and one sample of senesced leaves per tree.

Mature living fine roots (here defined as roots of ≤ 5mm in diameter) were excavated near to the coarse root of each sampled tree. They were sieved and washed with tap water. These samples contained not only fine roots of the target tree but also possibly of other plants as they were not able to be distinguished empirically. We, therefore, treated them as plot-level (i.e. plant community level) samples, not as individual tree samples in our study. Fine roots were, therefore, analysed for two replicates per species per plot only (n = 10 per plot).

A tree census was conducted, and 425 species (≥ 10 cm DBH) from 175 genera were identified from 2,155 trees across five logged forest plots. The species sampled for this study accounted for, on average, 26%, 41% and 53% of the species, genus and

family basal areas, respectively, in the logged plots. This enabled us to cover a broad taxonomic and functional type range from light-demanding pioneer to shade-tolerant late-successional species.

In the two old-growth forest plots in Maliau, the total number of stems, 882, comprised 239 species from 118 genera. In the two old-growth forest plots in Lambir, the total number of stems, 809, comprised 360 species representing 118 genera. The species sampled for this study accounted for, on average, 16%, 37% and 65% of the species, genus and family basal areas, respectively, in the old-growth plots.

Plot-level values were estimated from the species-level data by a nested weighting approach: first, each species was assigned the weight of its basal area proportion. Then, unsampled species within the same genus were assigned a genus-level mean, and finally unsampled species within the same families were assigned a family-level mean. We only weighted according to sampled families – unsampled families were ignited in calculating plot-level weighted mean concentrations. To increase the proportion of the sampled species in each plot, we combined species-level estimates from the plots of the same area and disturbance class, that is, we combined species-level data among logged plots, and among the two old-growth plots in Maliau. We did not combine the species-level data in the two old-growth plots in Lambir due to their strongly contrasting soil types.

Chemical analyses of plant tissues:

Concentrations of five macronutrient elements (N, P, K, Ca and Mg) and carbon (C) in each individual component were quantified at the chemistry laboratory in Forest Research Centre, in Sabah, Malaysia. First, all samples were oven dried at 50°C to constant weight for five days, and were then ground with a Thomas Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 100-mesh (212-μm) sieve. Branch samples including the bark were chipped to small pieces before grinding. Both green and senesced leaves included petioles.

Most of the protocols are described in Majalap and Chu (1992). Summary of the methods used are as follows. Each sample was digested following the sulphuric acid-hydrogen peroxide-lithium sulphate digest procedure for vegetation described in Allen (1989). Phosphorus in the digest was determined using the molybdenum-blue method described in Anderson and Ingram (1993) and read at 880 nm on a spectrophotometer (HITACHI UV-VIS, Tokyo, Japan), while K, Ca and Mg contents were measured on an atomic absorption spectrophotometer (GBC Scientific Equipment, Victoria, Australia). Total C and N contents (as total element contents) were determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany).

Soil sampling and analysis:

Within each 1 ha plot, two soil cores to the depth of 100 cm were collected and divided into six depth layers (0-5, 5-10, 10-20, 20-30, 30-50, 50-100 cm), and one soil pit dug up to 300 cm, and samples collected from 10 layers divided into 10 depth layers (0-5,

5-10, 10-20, 20-30, 30-50, 50-100, 100-150, 150-200, 200-250, 250-300 cm) on the pit walls. We then defined the depth of 0-30 cm as topsoil layer (Table 5.2), and 30-300 cm as subsoil layer (Table S5.2). We used the topsoil layer as a proxy for soil nutrient availability in this study, where fine roots were mostly limited to the top 30 cm of soil profile (Yoda, 1978). Soil sampling was done following the standard RAINFOR protocol (see http://www.rainfor.org/en/manuals; Quesada et al., 2010) and soil samples were air dried in the field. Following the removal of roots, detritus, small rocks and particles over 2 mm, samples were then sieved at 2 mm, and analysed for: total P (modified from Hedley et al., 1982), and C and N (Pella, 1990, Nelson and Sommers, 1996), exchangeable cations by the silver-thiourea method (Pleysier and Juo, 1980), and pH in water at 1:2.5, along with bulk density, and soil texture (the proportion of sand, silt and clay) at the University of Leeds, United Kingdom.

Estimation of NPP

Net primary productivity (NPP) is the rate of biomass synthesis that is used to form organic compounds in plants (Roy and Saugier, 2001). It is expressed as the difference between gross primary productivity (GPP) (i.e. total ecosystem photosynthesis) and autotrophic respiration, and can be quantified at the scale of an individual plant or ecosystem (Malhi et al., 2011). The following NPP components were quantified: canopy (leaves, twigs, reproductive parts), woody (stem, coarse roots and branch), and fine roots. NPP data for seven plots in Sabah was collected during 2012 to 2014, over a 24 month period in each plot, and are described in detail in Riutta et al. (2018), while the data for two plots in Sarawak was collected for 15 months between 2008 and 2010, and tree census was carried out every five years during 1992 to 2008

(Kho et al., 2013). The data were collected using standardized GEM protocols (Marthews et al., 2014, Malhi et al., 2021). Methods are described in detail in a manual available on the GEM website (http://gem.tropicalforests.ox.ac.uk, and in the site-specific papers (Kho et al., 2013, Riutta et al., 2018).

Estimation of leaf nutrient and C resorption rate:

During senescence substantial leaf mass loss occurs, mainly due to the resorption of nutrients and C (Vergutz et al., 2012); thus, disregarding mass loss leads to an underestimation of resorption by ~10% (van Heerwaarden et al., 2003). Calcium has been reported not to be resorbed due to its immobility (Vitousek and Sanford, 1986, Lambers et al., 1998). A global meta-analysis by (Vergutz et al., 2012) documented that Ca resorption was statistically indistinguishable from 0% resorption for all woody species. We thus adopted the approach depicted in Vitousek and Sanford (1986): senesced leaf nutrient content was corrected with the mass loss correction factor (MLCF), using Ca content as a reference value. Measured nutrient concentration was multiplied by the ratio of Ca concentration in green leaves and in senesced leaves averaged over the plot total leaf set.

Our mean leaf mass loss derived from the mean green to senesced leaf Ca ratio was 25.0±3.5%, which was slightly higher than the mean leaf mass loss of tropical evergreen woody angiosperms of 22.6% averaged from 31 global data points (Vergutz et al., 2012), which did not include any observations from Bornean forests.

Nutrient (x) resorption rate (%) was computed for each sample as

$$R_x = \left(1 - \frac{x_{senesced}}{x_{green}} MLCF\right) \times 100$$

(Eq. 1)

where *x* is an element of either N, P, K, Ca, Mg or C, R_x is the resorption rate of *x*, x_{green} is *x* concentration in green leaves, $x_{senesced}$ is *x* concentration in senesced leaves, and MLCF is the green to senesced leaf Ca ratio. The MLCF was calculated separately for each species in each plot, and the mean MLCF was 0.75±0.035 across plots.

Estimation of nutrient stoichiometry, uptake, requirement and use efficiency:

x stoichiometry was expressed as C:*x* ratio, that is, the ratio of C concentration to *x* concentration of nutrient *x* in each plot.

The following set of equations were used to calculate total nutrient requirement, total uptake (= requirement – resorption), nutrient use efficiency (NPP divided by requirement), and nutrient uptake efficiency (NPP divided by uptake) for each nutrient and each site (Eq. 1-5):

$$xRequirement\ (kg\ x\ ha^{-1}\ year^{-1}) = \left[\left(\frac{NPP_{canopy}}{C{:}x_{green}}\right)\right] + \left(\frac{NPP_{wood}}{C{:}x_{wood}}\right) + \left(\frac{NPP_{fine\ roots}}{C{:}x_{fine\ roots}}\right)$$

(Eq. 2)

II. *Canopy* II: *Woody* III: *Fine roots*

$$xUptake\ (kg\ x\ ha^{-1}\ year^{-1})$$

$$= \left[\left(\frac{NPP_{canopy}}{C{:}x_{green}}\right) \times (1\ - R_x)\right] + \left(\frac{NPP_{wood}}{C{:}x_{wood}}\right) + \left(\frac{NPP_{fine\ roots}}{C{:}x_{fine\ roots}}\right)$$

(Eq. 3)

I. *Canopy uptake* II: *Woody uptake* III: *Fine root uptake*

$$xUse\ Efficiencies\ (kg\ C\ per\ kg\ x\ ha^{-1}\ year^{-1})$$

$$= \frac{NPP_{green} + NPP_{wood} + NPP_{fine\ roots}}{xRequirement}$$

(Eq. 4)

$$xUptake\ Efficiencies\ (kg\ C\ per\ kg\ x\ ha^{-1}\ year^{-1})$$

$$= \frac{NPP_{green} + NPP_{wood} + NPP_{fine\ roots}}{xUptake}$$

(Eq. 5)

The above estimations depend on the assumption that nutrients used for NPP are offset by an equivalent amount of nutrients accrued from soil (and nutrient resorption) over the annual cycle. Nutrient use or requirement is the total stoichiometric requirement to build plant tissue, and nutrient uptake is the fraction of that demand that is not met through resorption and hence requires fresh uptake from soil or litter. This calculation assumed negligible resorption during the fine root senescence, or during conversion of live wood to heartwood, as very little is known about those two processes (see Chapter 4 for the analysis of wood resorption).

The NPP_{wood} was the sum of stem, branch, and coarse root production, while $C{:}x_{wood}$ was estimated solely using the branch C and *x* content. To reduce a systematic bias towards either underestimation or overestimation because C and *x* contents in wood differed in different parts of a whole tree, the correction factors of 0.792 (N), 0.796 (P), 0.847 (K), 1.531 (Ca), 1.226 (Mg) and 1.007 (C) were applied to C:*x* wood. These correction factors were derived by taking the mean of C and *x* content of all other woody components (sapwood at the bottom of the trunk, heartwood at bottom of the trunk, sapwood at the middle height of the trunk, heartwood at the middle height of the trunk, and coarse roots) except branches, and dividing this mean by the branch content (see Chapter 4 for the analysis of wood nutrient allocation).

Nutrient uptake can be considered as the sum of nutrient accrual in above- and belowground biomass, nutrient returns to the soil via litterfall, and foliar leaching from the canopy. Hiremath et al. (2002) reported that foliar leaching N loss is < 0.5% of total N uptake and P loss is 1.7-10.9 % of total P uptake. Freschet et al. (2010) also documented leaching accounted for less than 1% of leaf N pool, and no more than 0.01% of the leaf P pool. The influence of leaching on leaf nutrient status appeared generally negligible compared with leaf resorption (Frangi et al., 2005, Vergutz et al., 2012). We therefore excluded the potential effect of leaching in our study.

Statistical analyses:

To examine whether the variation in nutrient dynamics was related to logging

disturbance gradient, we used the basal area of tree stand (Table 5.1) as a proxy for the level of disturbance. We then applied a linear regression with basal area as the explanatory variable and nutrient resorption, requirement, uptake, use efficiency, uptake efficiency, resorption contribution to total requirement, and resorption contribution to canopy requirement as response variables. We ran a separate model for each response variable and each nutrient combination.

Statistical analyses were performed in the R programing language version 4.0.4 (R Core Team, 2021), the packages 'ggplot2' (Wickham, 2016) and 'ggtern' (Hamilton and Ferry, 2018). To examine if the fractional allocation of the nutrient requirement and nutrient uptake to the different organs (canopy, woody and fine root components) varied between heavily logged (Hlog), moderately logged (Mlog) and old-growth forests, we ran a linear model for compositional data (R package 'compositions'; van den Boogaart et al., 2021), separately for each nutrient.

RESULTS

Resorption

The mean (±SE) resorption rates of mobile elements across plots were 46.9±2.4% (N), 62.1±3.6% (P), 57.8±3.2% (K), 16.2±4.2% (Mg) and 22.0±4.9% (C) respectively (Fig. 5.1). While there was considerable variation among plots, there was no clear pattern

related to the disturbance gradient for N P, Mg and C (Fig. 5.1). Resorption rate decreased towards higher disturbance for K (regression with basal area was significant: r^2=0.632, p=0.010). While Ca was assumed to not be resorbed, and the data therefore forced to zero, some of Mg and C efficiencies show negative values, suggesting that Mg and C concentrations of some senesced leaves were higher than that of the green leaves.

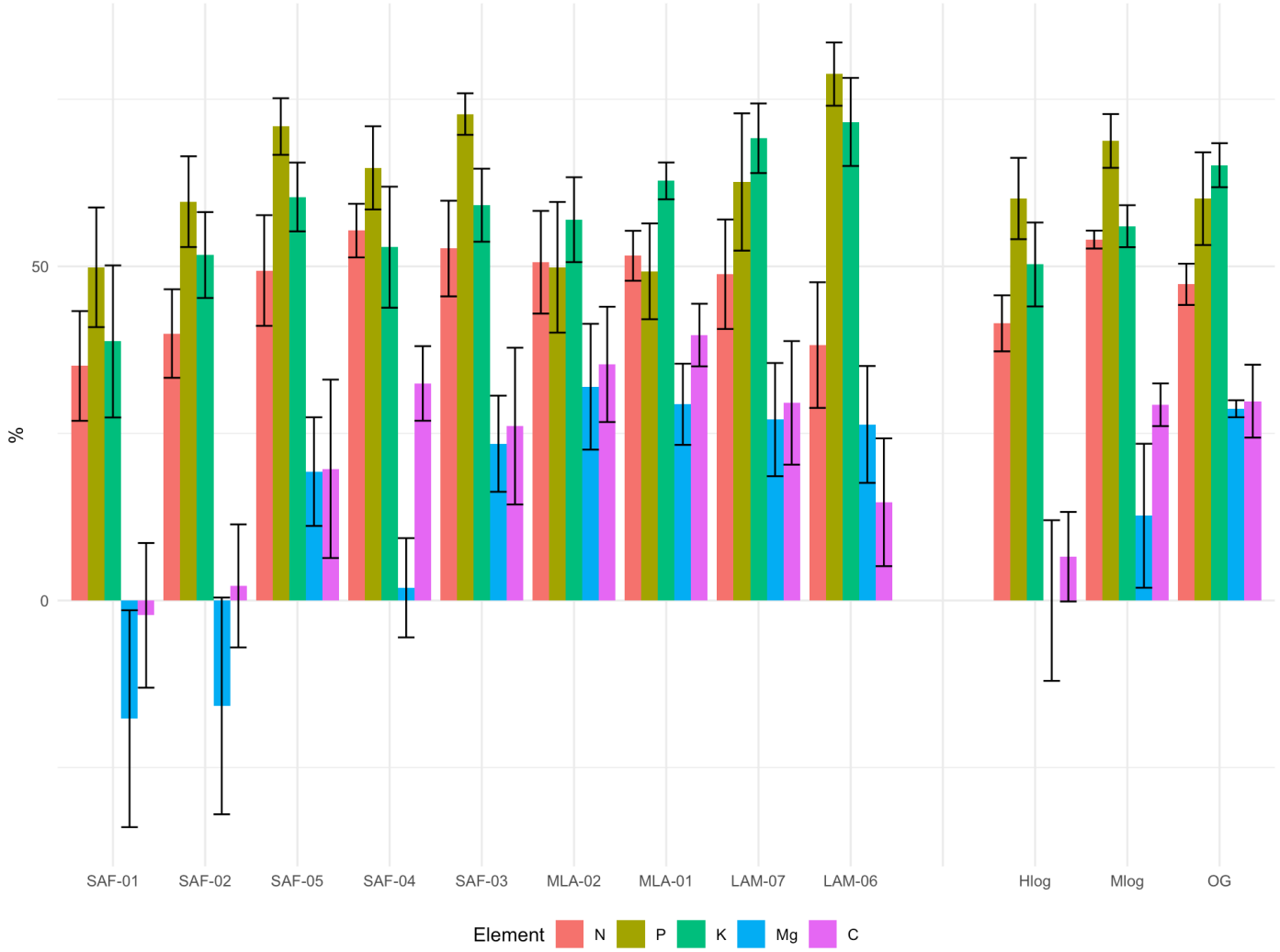

50
0
%
SAF-01
SAF-02
SAF-05
SAF-04
SAF-03
MLA-02
MLA-01
LAM-07
LAM-06
Hlog
Mlog
OG
Element
N
P
K
Mg
C

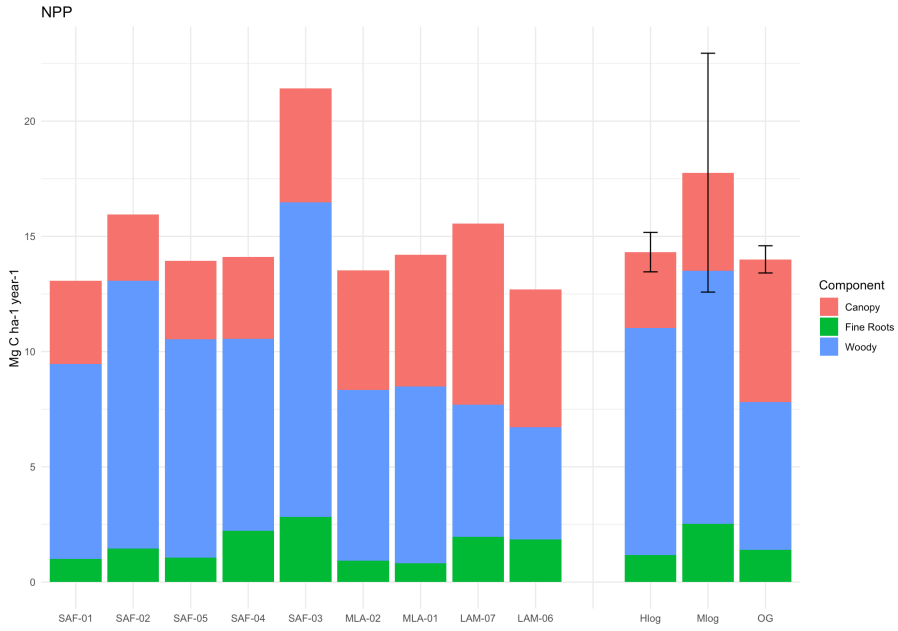
Figure 5.1 Resorption rates (%±SE) (Eq. 1) of six elements (N, P, K, Ca, Mg and C) along a disturbance gradient (disturbance level decreases on x-axis).

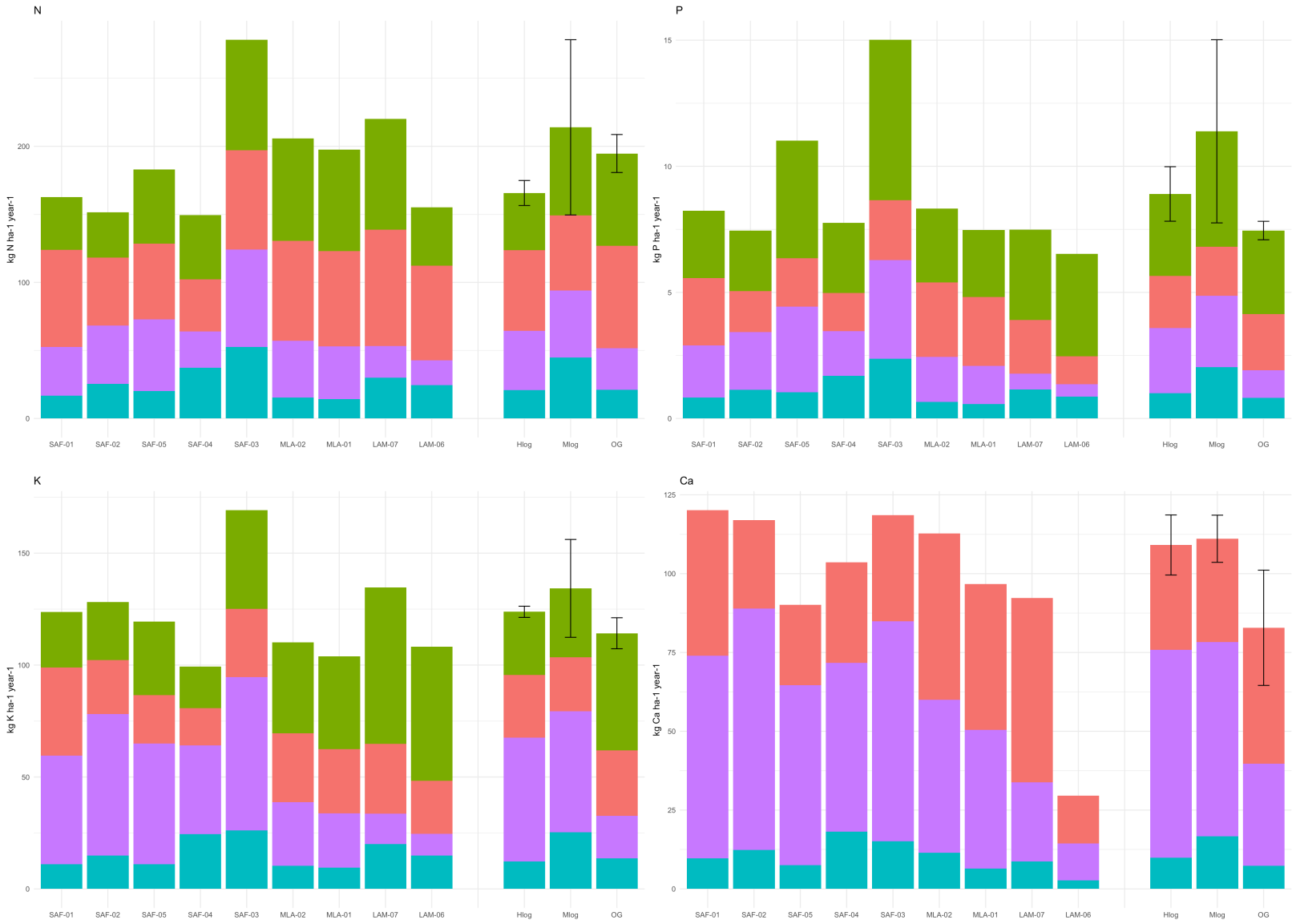
The values were averaged within each plot (*n* = 15 trees per plot). The three bars on the right refer to the mean of each disturbance group of heavily logged (Hlog: SAF-01, SAF-02 and SAF-05), moderately logged (Mlog: SAF-04 and SAF-03) and old-growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06). For plot descriptions, see Table 5.1. Resorption of Mg and C showed negative values in some plots, but only SEs are shown in this figure.

The resorption rates had great variation among old-growth plots, with the highest resorption rate found in LAM-06: P (78.8±4.7%) followed by K (71.6±6.6%), but with relatively lower N resorption rate than in other plots (Fig. 5.1). Within heavily logged (Hlog) plots, SAF-05 had active resorption for every element, whereas resorption was the smallest among all plots in the most heavily disturbed SAF-01: 35.1±8.2% for N, 49.9±9.0% for P and 38.8±11.4% for K respectively.

Nutrient requirement, uptake and allocation

With the exception of SAF-03, the total NPP was similar across the plots and forest types (Fig. 5.2). Similarly, there was no pattern in total nutrient requirement or uptake along the logging disturbance gradient (Fig. 5.2), except for K, which showed higher uptake towards more disturbed sites (regression with basal area was significant: r^2=0.533, p=0.025). Nutrient allocation to canopy, woody and fine root varied, however, both among nutrients and forest types (Fig. 5.2, Fig. 5.3).




N
kg N ha-1 year-1
0
100
200
P
kg P ha-1 year-1
0
5
10
15
K
kg K ha-1 year-1
0
50
100
150
Ca
kg Ca ha-1 year-1
0
25
50
75
100
125
SAF-01
SAF-02
SAF-05
SAF-04
SAF-03
MLA-02
MLA-01
LAM-07
LAM-06
Hlog
Mlog
OG

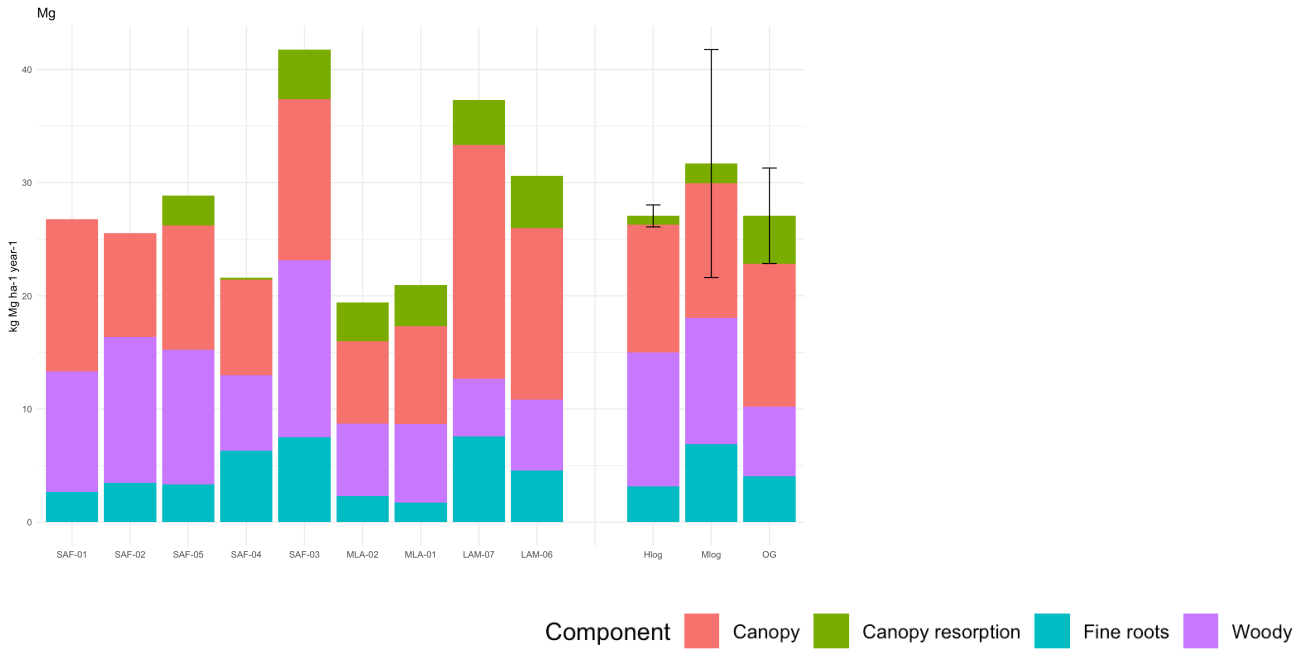
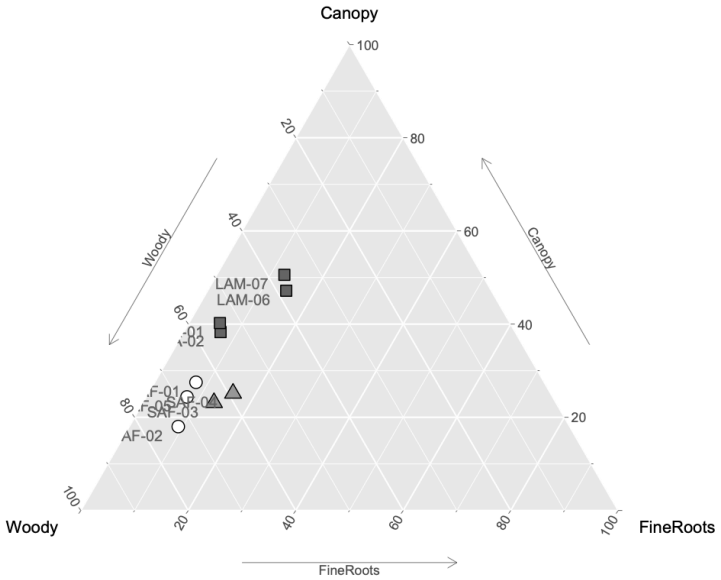


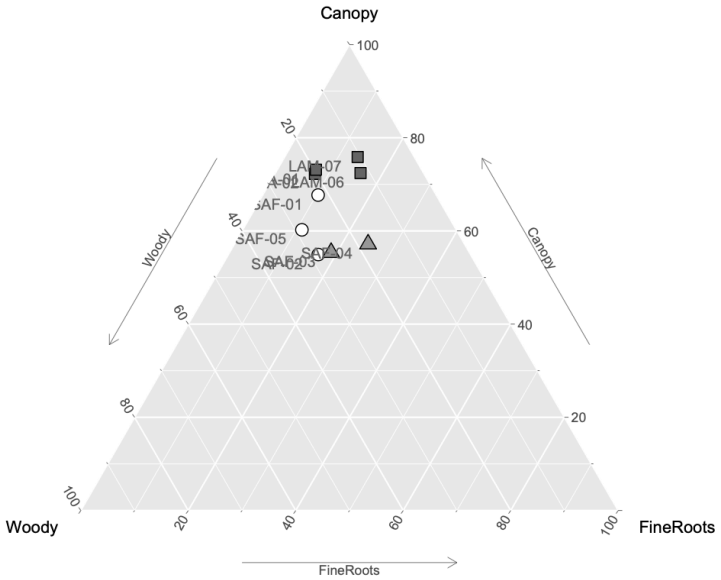
Figure 5.2 Net primary productivity (NPP) (Kho et al. 2013; Riutta et al. 2018), and nutrient requirement (Eq. 2) along a disturbance gradient (disturbance level decreases on x-axis), partitioned into components: canopy resorption, canopy, woody and fine roots.

The bars represent nutrient uptake from soil (Eq. 3) if canopy resorption is excluded. Note that calcium resorption is assumed to be zero. The values were averaged within each plot. The three bars on the right refer to the mean of each disturbance group of heavily logged (Hlog: SAF-01, SAF-02 and SAF-05), moderately logged (Mlog: SAF-04 and SAF-03) and old-growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06). For plot descriptions, see Table 5.1.

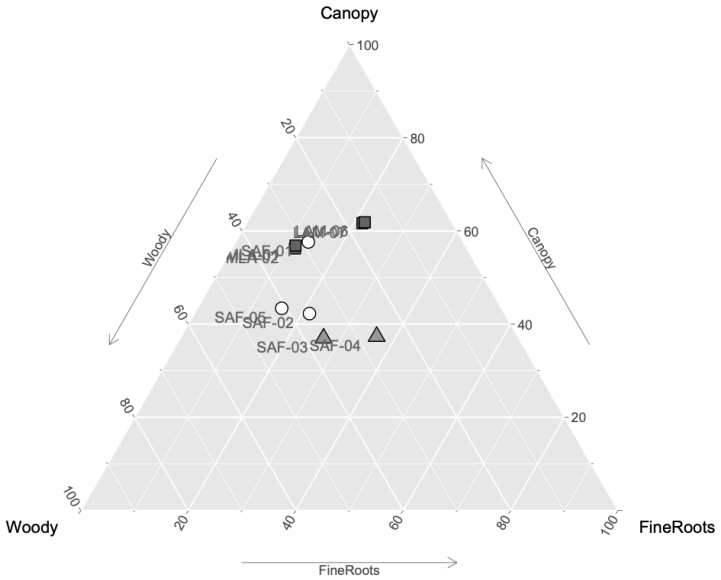
NPP



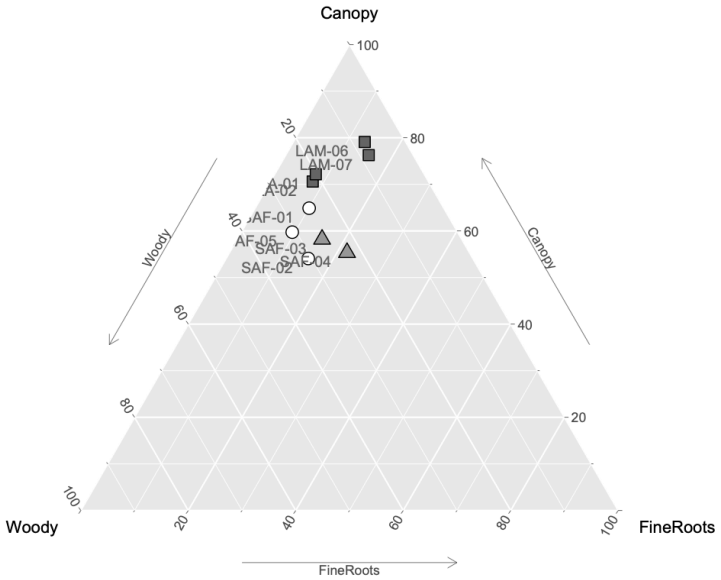
N requirement



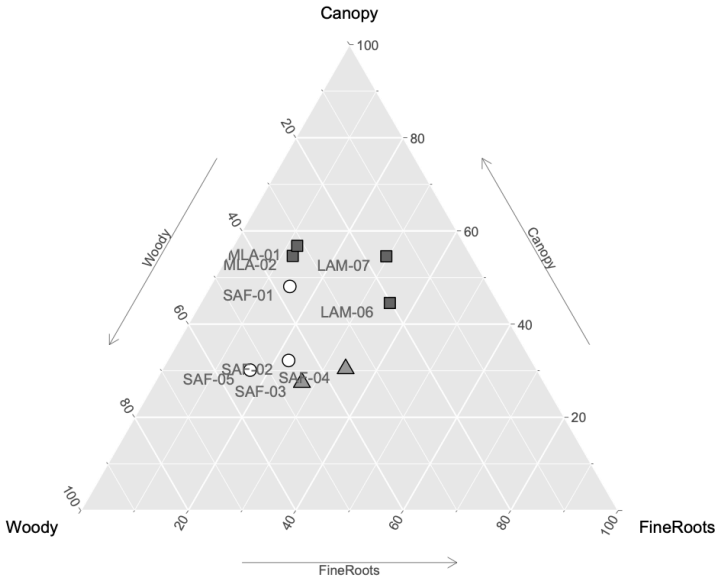
N uptake



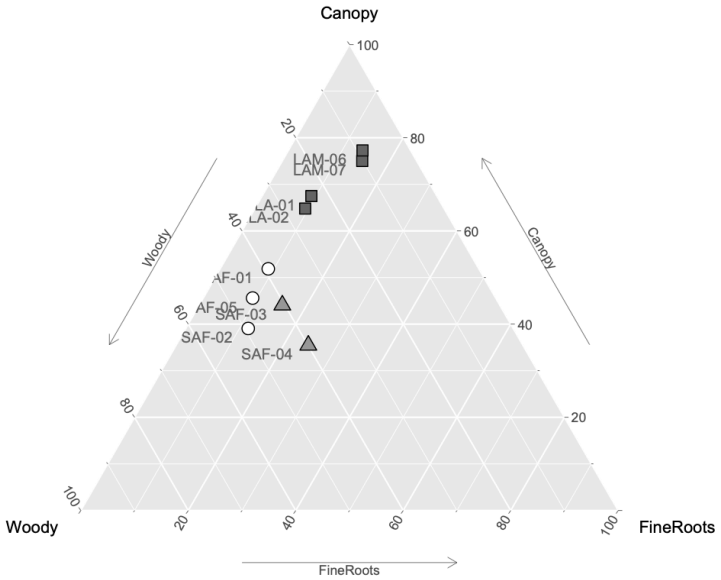
P requirement



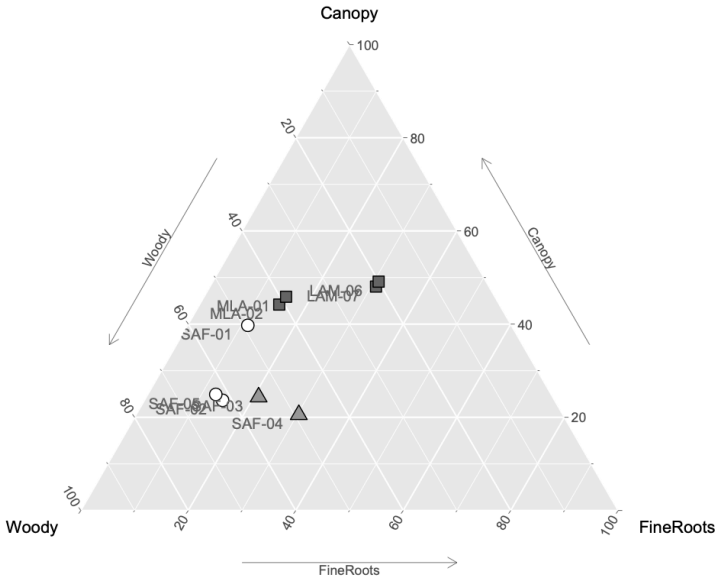
P uptake



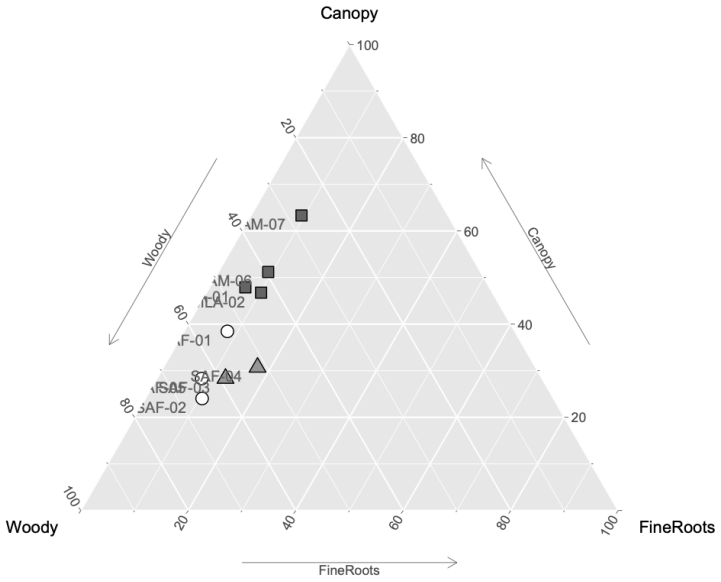
K requirement



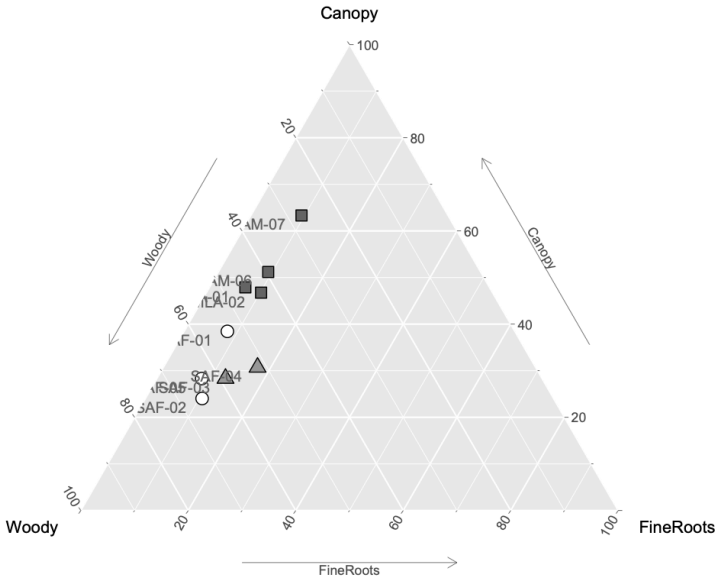
K uptake



Ca requirement



Ca uptake



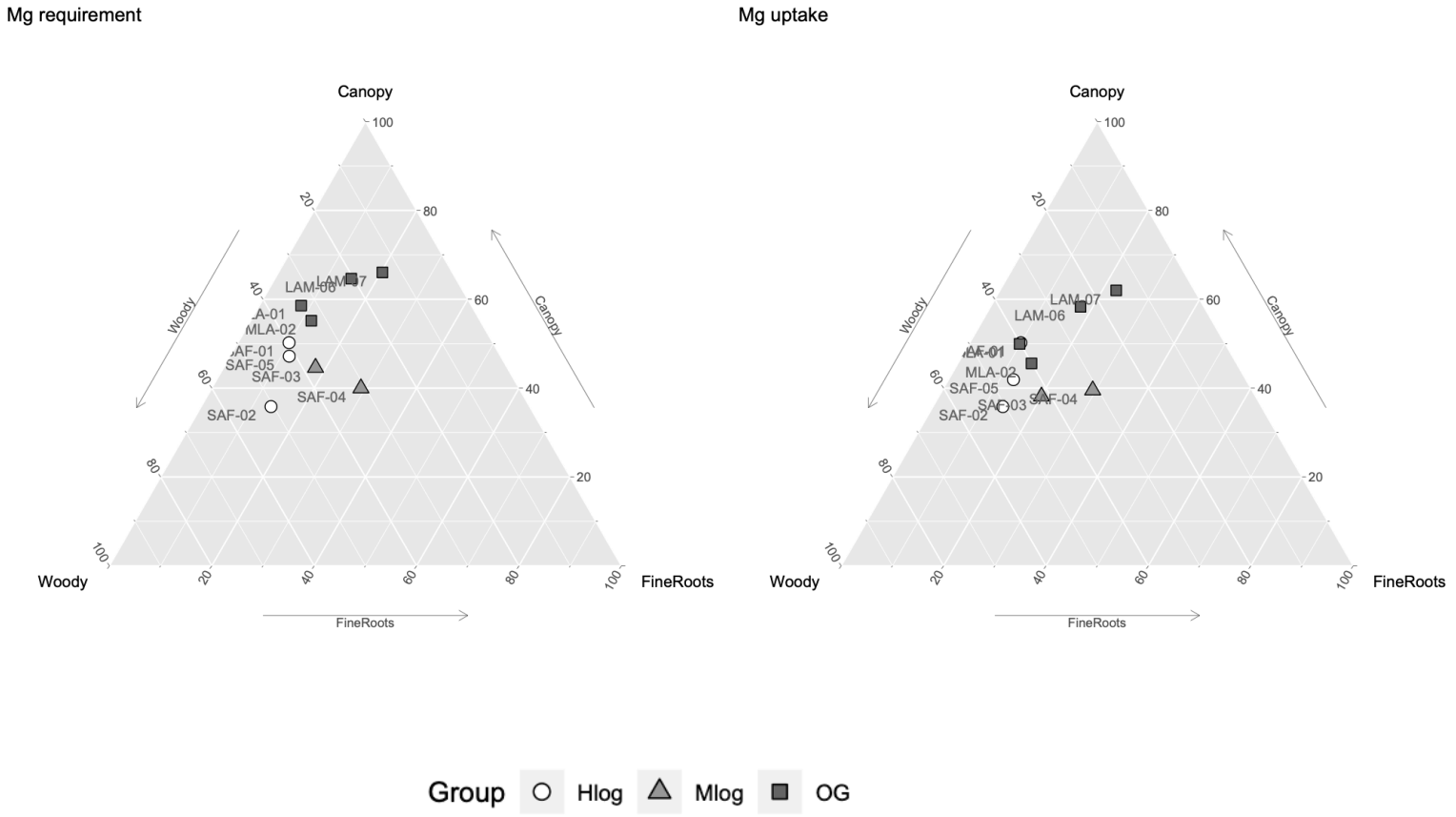


Figure 5.3 Ternary diagrams of the fractional allocation (% of total) of net primary productivity (NPP) and nutrient requirement (nutrient uptake + canopy resorption) to three components: canopy, woody and fine roots.

Each data point is one forest plot, grouped into heavily logged (Hlog: SAF-01, SAF-02 and SAF-05), moderately logged (Mlog: SAF-04 and SAF-03) and old-

growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06). For plot descriptions, see Table 5.1. Top row shows NPP and the other rows shows nutrient allocation, with resorption included (left panels) and excluded (right panels), which represents nutrient uptake from the soil. Note that calcium does not have resorption so the two panels are identical. In all panels, OG plots differ from both Hlog and Mlog plots, which do not differ from each other (compositional analysis, $p<0.05$); except for N uptake (right panel, second row), where all three forest types differ from one another, and Mg uptake (right panel, bottom row), where OG and Mlog plots differ but OG and Hlog plots do not.

Nitrogen, P and Mg were predominantly allocated to the canopy and little to the wood across plots, whereas the woody allocation of K and Ca requirement was as large as that of the canopy in logged plots (Fig. 5.2, Fig. 5.3). The exceptionally large N, K and Mg requirement in SAF-03 was primarily driven by the high NPP and lower C to nutrient ratios. All old-growth plots had fairly similar P requirement, while P requirement in logged plots was highly variable, with high P requirement in SAF-05 and SAF-03, which also had with high resorption contribution (Table 5.3). There was less K requirement in the wood in old-growth plots, whereas their requirement on the canopy was substantially supplied by resorption. In addition to K, lower N and P requirement in old-growth plots was also largely compensated by resorption, although the proportion greatly varied within these plots. The discrepancy on the contribution of P resorption to P requirement between LAM-06 (62.3%) and MLA-01 (35.6%) was exceptionally large (Table 5.3), while there existed the slight contrast between heavily logged (Hlog) and moderately logged (Mlog) plots. It was worth noting that within old-growth plots the woody allocation of all elements in Lambir was lower than that in Maliau. In addition, the great discrepancy between LAM-07 and LAM-06 (among the lowest value) was Ca requirement, where the former plot had clay and the latter plot had sandy soil.

Table 5.3 The contribution of nutrient resorption (%) to total nutrient requirement in each plot and disturbance group (%±SE).

Plot code	N	P	K	Mg
SAF-01	23.77	32.35	20.11	0.00
SAF-02	21.95	32.28	20.20	0.00
SAF-05	29.75	42.37	27.53	9.10
SAF-04	31.65	35.84	18.75	0.77
SAF-03	29.16	42.37	26.08	10.47
MLA-02	36.58	35.21	36.93	17.65
MLA-01	37.73	35.55	39.92	17.20
LAM-07	37.04	47.77	51.89	10.65
LAM-06	27.68	62.31	55.35	15.17
Hlog	24.91±2.36	35.58±3.35	22.81±2.46	2.84±3.03
Mlog	29.81±1.25	38.31±3.27	21.87±3.66	5.21±4.85
Old-growth	34.61±2.37	44.53±6.40	45.74±4.48	15.57±1.60

Disturbance level decreases in descending order. The values were averaged within each plot, and then averaged in each disturbance group of heavily logged

(Hlog: SAF-01, SAF-02 and SAF-05), moderately logged (Mlog: SAF-04 and SAF-03) and old-growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06) forests. For plot descriptions see Table 5.1.

Nutrient resorption contributed more towards meeting the canopy nutrient requirement in the undisturbed sites compared with the more heavily disturbed sites (regression with basal area was significant) for K (r^2=0.536, p=0.025) and Mg (r^2=0.619, p=0.012). Nutrient resorption provided 47.3 ±3.1% (N), 60.1±6.9% (P), 64.2±3.6% (K), and 25.2±3.5% (Mg) of canopy requirement (the sum of canopy resorption and canopy uptake) of in old-growth forests, and 46.5±3.9% (N), 63.6±4.1% (P), 52.6±3.8% (K) and 8.9±5.1% (Mg) in logged forests.

Similar pattern was found for the nutrient resorption contribution to the total nutrient requirement, were the resorption contribution increased towards the undisturbed sites for N (r^2=0.493, p=0.035), K (r^2=0.701, p=0.005) and Mg (r^2=0.769, p=0.002). The resorption contribution of P was not related to the level of logging disturbance. In old-growth forest, resorption provided 34.6±2.4% (N), 44.5±6.4% (P), 45.7±4.5% (potassium [K]), and 15.6±1.6% (magnesium [Mg]) of the nutrient requirement, while in logged forest the corresponding values were 27.3±2.2% (N), 35.7±2.3% (P), 21.7±1.8% (K) and 2.5±2.3% (Mg), respectively.

The NPP was mostly allocated to the wood in Hlog and Mlog plots, while it was equally distributed to both the canopy and wood in old-growth plots (Fig. 5.2, Fig. 5.3, compositional analysis confirmed the significantly different partitioning in old-growth vs. Mlog and Hlog plots: p=0.001, while Mlog and Hlog plots did not differ from each other: p=0.314). Compared with NPP, the partitioning of the nutrient requirement shifted towards the canopy, particularly prominent in N and P (Fig. 5.3: left panels),

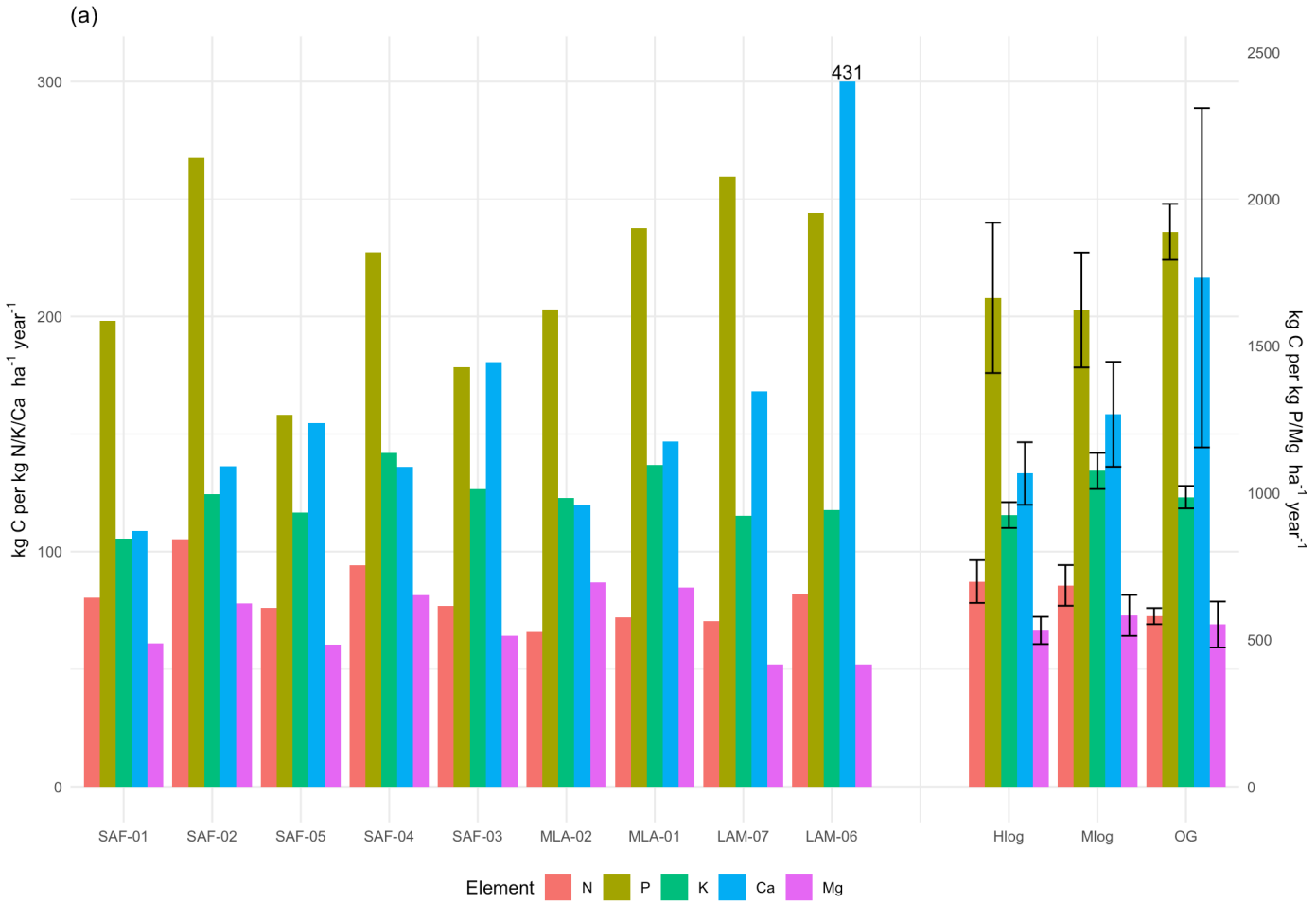
making cation requirement in logged plots evenly partitioned between the canopy and wood. Although the fraction of fine roots was considerably low, SAF-04 showed the larger fraction than other plots for P, K and Mg.

When resorption rate was not taken into account, the trend reversed back towards the wood making the requirement fraction more even between the canopy and wood (Fig. 5.3: right panels). This suggests that higher resorption rate offsets lower nutrient requirement given that the right panels in Fig. 5.3 represents the net uptake from soil. In some plots like SAF-04 (except for K), fine root distribution was almost equivalent to that of the canopy and wood (except for K), shifting the allocation closer to equal partitioning among three components.

Nutrient partitioning among canopy, woody and fine root components differed between forest types for all nutrients (p-value of the compositional analyses <0.05), both for the nutrient requirement and nutrient uptake (Fig. 5.3). Compared with old-growth forests, logged forests allocated more nutrients towards wood, at the expense of canopy allocation. Nutrient allocation to fine roots was similar in both forest types. In every case, the old-growth plots differed from both the Mlog and Hlog plots, which did not differ from each other, except for N uptake, where all three forest types differed from one another, and Mg uptake, where old-growth plots differed from Mlog plots but not from Hlog plots.

Nutrient use efficiency and nutrient uptake efficiency

Phosphorus use efficiency was 10–20 times larger than N, K and Ca use efficiencies (Fig. 5.4a). Nitrogen use efficiency was homogenous across disturbance groups, whereas P and K use efficiencies were particularly high in old-growth plots, predominantly driven by Lambir plots. Calcium-limited LAM-06 was the most Ca efficient plot. While SAF-05 had substantially high soil P (Table 5.2), it had a substantially low P use efficiency (Fig. 5.4a). In contrast, P-poor Lambir plots showed substantially high P use efficiency. There was, however, no significant relationship between basal area and the use efficiency for any nutrient, indicating that the variability among plots was not related to logging disturbance. Nutrient use efficiency (Fig. 5.4a) and nutrient uptake efficiency (Fig. 5.4b) showed broadly similar patterns across the plots and nutrients.


(a)
431
kg C per kg N/K/Ca ha-1 year-1
kg C per kg P/Mg ha-1 year-1
0
100
200
300
500
1000
1500
2000
2500
SAF-01
SAF-02
SAF-05
SAF-04
SAF-03
MLA-02
MLA-01
LAM-07
LAM-06
Hlog
Mlog
OG
Element
N
P
K
Ca
Mg

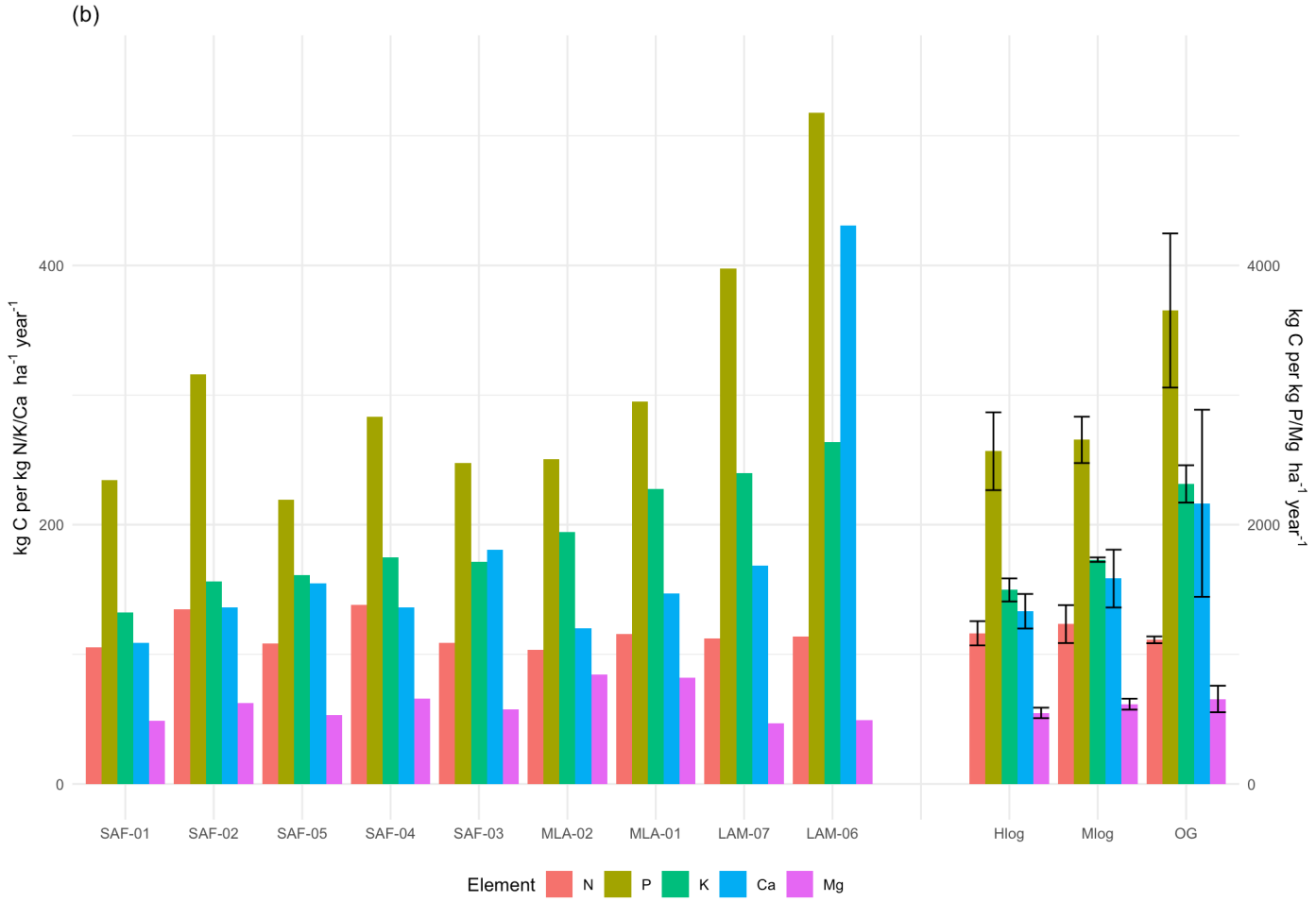


Figure 5.4 a) Nutrient use efficiencies (net primary productivity divided by nutrient requirement, Eq. 4) and b) nutrient uptake efficiencies (net primary productivity divided by nutrient uptake, Eq. 5) along a disturbance gradient

(disturbance level decreases on x-axis). The values were averaged within each plot. The three bars on the right refer to the mean of each disturbance group of

heavily logged (Hlog: SAF-01, SAF-02 and SAF-05), moderately logged (Mlog: SAF-04 and SAF-03) and old-growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06) forests. For plot descriptions, see Table 5.1. Note that P and Mg are on the left axis.

Chapter 5

DISCUSSION

Resorption rate

Our results correspond with the general theory and previous studies, that about half of N, P, and K are resorbed (Huang et al., 2007, Yuan and Chen, 2009, Chapin et al., 2011). A global meta-analysis by Vergutz et al. (2012) reported resorption rates of 49.5% (N), 59.3% (P), 51.9% (K), 0.9% (Ca), 14.5% (Mg) and 18.1% (C), respectively, for tropical evergreen woody angiosperms, which were corrected for MLCF. Despite the small, non-zero resorption estimate for Ca, Vergutz et al. (2012) concluded that it statistically indistinguishable from 0% for all woody species. These resorption estimates, which did not include any data from Borneo, are very similar to the ones in our study.

Our results were relatively consistent with the general trends that tropical forests are characterized by the high rate of P resorption relative to N (Fig. 5.2), low litter and foliar P content (Table S5.2), and high foliar N:P ratios (McGroddy et al., 2004, Townsend et al., 2007). Either the low tissue P concentrations (Table S5.2) or high P resorption indicates that P is a key limiting nutrient (Dalling et al., 2016). Soil P limitation has been frequently reported in tropical forests (Reich and Oleksyn, 2004, Vitousek et al., 2010). In general, the highly weathered soils in the lowland tropics are depleted of rock-derived nutrients like P, and low P availability and total P in these soils are further exacerbated by long periods of leaching and intense adsorption or

occlusion of P with iron and aluminum oxides (Uehara and Gillman, 1981, Baillie, 1996).

There is a tendency that resorption rate decreases with increasing leaf nutrient content and vice versa (Kobe et al., 2005, Vergutz et al., 2012). For example, N_2-fixing *Acacia* species has high leaf N concentration, but low N resorption of 19% (Wright and Westoby, 2003). Higher leaf N concentrations in Hlog plots (Table S5.2) are also consistent with lower resorption rates (Fig. 5.1). Such results indicate that resorption may be an adaptive trait with great flexibility (Vergutz et al., 2012).

Resorption by other organs such as stem and fine roots was not considered in our study. Compared to leaves, the senescence and resorption mechanisms of stems and roots are not well understood. Tropical humid trees, however, might be less efficient in sapwood resorption, which is compensated for by efficient foliar resorption (Lambert and Turner, 1989; see Chapter 4 for the analysis of wood resorption). Resorption rate of fine roots is lower than that of leaves (Aerts, 1990, Freschet et al., 2010), but ideally, resorption by stems and fine roots should be incorporated into this assessment.

Calcium, Mg and C concentrations in most senesced leaves were higher than that of the green leaves (Table S5.2). This pattern appears not exceptional in lowland tropical forests, as (Frangi et al., 2005) report that green leaves have slightly higher or lower Mg concentration than senesced leaves due to its low mobility, in addition to Ca in green leaves to be absolutely the lowest, in erect forests in Argentina. We, therefore,

assume that our case is related to known Mg adsorption (Price, 2006) onto surfaces of senesced leaves on soils.

There is likely to be an uncertainty in our resorption estimates based on the senesced to green leaf Ca ratio, as large portions of Ca leaching are observed in leaves (Tukey, 1970, Lambers et al., 1998). The rate of leaching, however, is likely to have no effect on resorption estimates appreciably (Freschet et al., 2010). A global meta-analysis by Vergutz et al. (2012) reports no relationship between mean annual precipitation, which is assumed to correlate with the leaching rate, and Ca resorption. Nevertheless, ideally monitoring the measurement basis of preselected leaves during senescence minimises such an uncertainty (van Heerwaarden et al., 2003).

Nutrient dynamics along the logging disturbance gradient

The role of the resorption is highlighted when it is examined as part of the ecosystem nutrient budget. While absolute resorption rates have been commonly reported, we are not aware of previous estimates of how much of the total or canopy nutrient requirement can be met through resorption, which our whole nutrient budget approach allows. We found the resorption contributed 44.5±6.4% and 45.7±4.5% of the total nutrient requirement for P and Mg, respectively, and 34.6±2.2% for N in old-growth plots. The resorption contribution to total nutrient requirement and/or canopy requirement increased with decreasing disturbance for N, K and Mg.

The patterns in nutrient dynamics varied among plots and among the nutrients. However, we did not find a clear trend in the nutrient requirement, uptake, or nutrient use efficiency related to logging disturbance. Nitrogen use efficiency appeared consistent across disturbance groups and more constrained than other elements. Phosphorus use efficiency was 10–20 times larger than N-, K- and Ca use efficiencies (Fig. 5.4a). The broad trends emerging from differences of resorption rates, nutrient uptake and nutrient use efficiencies can be attributed to a trade-off between nutrient acquisition and conservation. Resource acquisitive species optimize nutrient acquisition via uptake, while conservative species reduce nutrient losses via resorption and protection against leaching, which is a widely known trade-off (Aerts, 1990, Reich et al., 1997) in the leaf economics spectrum (LES; Wright et al., 2004). The former fast-growing species with higher short-term productivity per leaf mass tend to dominate in fertile soils, while the latter slow-growing species tend to dominate in infertile soils (Chapin, 1980, Aerts, 1995). The former includes light-demanding species which invest resources in foliage to increase growth rates, while the latter includes shade-tolerant species which invest in structural stem and leaf defences (Kitajima and Poorter, 2010).

Total P requirement was more uniform in old-growth than logged plots, which showed considerable plot-to-plot variation (Fig. 5.2), while the contribution of P resorption to total P requirement varied more in old-growth plots than in logged plots (Table 5.3). However, the large variability in P dynamics across the plots was not related to the

logging intensity. The most P- and K-limited SAF-04 also had among the highest P and K uptake efficiencies (Fig. 5.4b), while the resorption rates and use efficiencies of P and K were moderate (Fig. 5.1, Fig. 5.4a). These suggest that plants may not be required to increase nutrient use efficiency when the availability of soil nutrients or uptake efficiencies is sufficiently large. The relationship with soil nutrient availability will be further explored in Chapter 6.

Calcium could be an important growth-limiting element, evidenced by Ca fertilisation that increases net photosynthesis rate in Brazilian Amazonia (Silva et al., 2008). In our study, soil Ca and Ca uptake were mostly limited in SAF-03 and LAM-06, most likely due to their soil texture type, but not in any Hlog plots (Table 5.1, Fig 5.2), indicating logging effect on Ca limitation appeared marginal. Previous studies, however, demonstrate the complexity of Ca limitation following disturbance. Calcium cycling in forests may be susceptible to biomass loss and disturbance as Ca accumulates in woody biomass (McGrath et al., 2001)., and repeated timber harvesting have been shown to cause substantial loss of soil Ca (e.g., Brouwer and Riezebos, 1998, Zech and Drechsel, 1998). In contrast, selective logging may increase soil availability of base cations over long periods of time due to increased mineralisation and decreased plant uptake (McNabb et al., 1997). Atmospheric deposition may also replenish depleted soil Ca (Vitousek and Sanford, 1986, Schroth et al., 2001). In Borneo, however, serious Ca deficiency has been reported. Harvest-related losses accounts for 19% of the total Ca in the ecosystem and soil to 50 cm depth in Sabah (Nykvist, 1997). The loss of Ca via leaching exceeds the annual input of Ca via wet deposition

(Grip et al., 1994), which is below 2 kg ha^{-1} yr^{-1} in Sabah (Nykvist, 2000).

Partitioning of nutrient requirement and uptake among canopy, wood and fine roots

To our best knowledge, this study and another recent study in Brazil (M. Scalon et al., unpublished manuscript) are the first attempts to combine NPP and nutrient stoichiometry across organs to partition nutrient requirement and uptake, while the existing literature focuses on nutrient stocks. A large fraction of nutrient requirement was allocated to the canopy in old-growth forests, whereas it was more evenly allocated to both the canopy and woody components in logged forests. Nutrient requirement allocation to fine roots appeared relatively invariant across plots. These patterns strongly mirror those of the allocation of NPP, with a shift in allocation towards woody productivity at the expense of canopy productivity in logged forests (Riutta et al., 2018). Differences in NPP allocation and resorption rates, rather than differences in nutrient stoichiometry among organs, drive the variability among plots.

When resorption contribution was not taken into account, the nutrient partitioning was more even between the canopy and wood – this represents the allocation of nutrients from soil uptake. This suggests that higher resorption rate offsets lower nutrient uptake.

Chapter 5

CONCLUSIONS

To our knowledge, this study is the first attempt at coupling NPP and nutrient stoichiometry to estimate nutrient requirement and its allocation to tree organs, nutrient uptake, and nutrient use efficiencies of five macronutrients, and the most extensive report to date on nutrient concentrations measured simultaneously in leaf, wood and fine root tissues in tropical forests. These are also the first estimates of resorption rates in disturbed forest ecosystems in Southeast Asia. Considering the extensive number of analysed samples: 495 tree components as well as soil samples across nine plots for the observation of six elements, these results have implications for global ecology, as nutrient capital and availability vary at the global scale (Hedin et al., 2003, McGroddy et al., 2004). A gradient of logging disturbance also helps us understand the nutrient dynamics in tropical regrowth forests, which represents ~30% of the total tropical forest area (Pan et al., 2011).

Our study demonstrates substantial variation in nutrient uptake and allocation across plots, while some consistent patterns emerge along a disturbance gradient. Nutrient resorption contributed more to the nutrient requirement in old growth forests than in logged forests. Nitrogen use efficiency appeared consistent across disturbance groups while P- and K use efficiencies were particularly high in old-growth plots.

The study focused on Malaysian Borneo, however, further sites are needed across the tropics, for example, within the Global Ecosystem Monitoring (GEM) network (http://gem.tropicalforests.ox.ac.uk) using a standardised protocol. As early nutrient studies suggest that tropical forests and soils should not be categorised as a single

entity (Vitousek and Sanford, 1986, Proctor, 1987, Richter and Babbar, 1991), the spatial heterogeneity of nutrient status is expected across the tropics.

Acknowledgements

This paper is a product of the Global Ecosystems Monitoring (GEM) network. We thank the Forest Research Centre, Sabah Forestry Department: the laboratory team for extensive chemical analyses, Mr Joel Dawat, Mr Postar Miun and Mr Bernadus Bala Ola for species identifications. We also thank Mr MinSheng Khoo and the field teams in the Stability of Altered Forest Ecosystems (SAFE) Project, Maliau Basin Studies Centre and Lambir Hills National Park for the indispensable assistance during the field measurements. Mr Martin Gilpin for chemical analysis of soil at the University of Leeds. We are grateful to Dr Lindsay Flynn Banin and the University of Leeds for data on soil nutrients on two plots in Lambir Hills National Park. The SAFE Project is generously supported by the Sime Darby Foundation, Sabah Foundation (Yayasan Sabah), Benta Wawasan and Sabah Forestry Department. We acknowledge the Sabah Biodiversity Centre, Maliau Basin Management Committee, and Forest Department Sarawak for permitting research in the SAFE Project (Access Licence: JKM/MBS.1000-2/2 (187)), Maliau Basin Conservation Area, and Lambir Hills National Park (Permit no. NCCD.907.4.4(JLD.10)-117 and park permit no. 66/2014) respectively.

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SUPPORTING INFORMATION

Table S5.1. Proportion of sampled basal area (BA)

Plot code	BA total m^2 ha^{-1}	BA of sampled families	BA of sampled genera	BA of sampled species	Sampled family proportion	Sampled genus proportion	Sampled species proportion
SAF-01	7.31	4.68	3.40	2.07	0.64	0.46	0.28
SAF-02	12.20	7.44	7.15	5.85	0.61	0.59	0.48
SAF-05	13.89	8.52	5.81	4.34	0.61	0.42	0.31
SAF-04	19.65	4.73	2.64	0.21	0.24	0.13	0.01
SAF-03	23.35	13.33	10.88	5.09	0.57	0.47	0.22
MLA-02	34.72	25.64	9.36	3.82	0.74	0.27	0.11
MLA-	41.30	32.15	19.71	9.19	0.78	0.48	0.22

01							
LAM-07	31.84	13.83	12.49	5.99	0.43	0.39	0.19
LAM-06	41.07	27.13	13.87	5.17	0.66	0.34	0.13

Table S5.2. Basal area weighted mean concentrations (± 1 SE) of nutrients of N, P, K, Ca, and Mg, and carbon (C) in green leaves, senesced leaves, branches and fines roots.

Plot code	**N (%)**	**P (mg/g)**	**K (mg/g)**	**Ca (mg/g)**	**Mg (mg/g)**	**C (%)**
			Green leaves			
SAF-01	1.37±0.43	0.68±0.46	8.27±1.40	6.84±1.57	1.96±0.64	44.33±0.99
SAF-02	1.62±0.40	0.76±0.30	10.39±1.31	3.65±0.88	1.75±0.59	45.69±0.82

SAF-05	1.55±0.47	1.21±0.70	9.46±1.74	5.67±1.84	2.42±0.84	46.77±1.43
SAF-04	1.12±0.33	0.54±0.39	4.18±0.87	4.59±1.29	1.04±0.40	46.19±0.74
SAF-03	1.40±0.32	0.76±0.46	7.09±1.32	3.31±0.99	2.03±0.56	45.66±0.93
MLA-02	1.43±0.36	0.58±0.30	6.45±0.83	5.55±0.82	1.31±0.41	47.79±0.78
MLA-01	1.40±0.36	0.57±0.31	6.84±1.35	5.18±0.79	1.28±0.37	47.94±0.76
LAM-07	0.93±0.21	0.40±0.16	5.10±0.86	2.80±0.61	1.20±0.52	47.75±0.42
LAM-06	0.86±0.30	0.38±0.28	7.46±1.28	1.24±0.56	1.66±0.37	45.75±0.76
			Senesced leaves			
SAF-01	0.85±0.36	0.28±0.26	4.37±1.07	7.53±1.15	2.23±0.79	43.32±0.95
SAF-02	0.84±0.27	0.21±0.20	4.09±1.25	3.88±0.88	1.86±0.81	44.73±0.97
SAF-05	0.87±0.34	0.37±0.27	4.03±1.07	8.37±1.49	2.42±0.83	44.15±0.97
SAF-04	0.77±0.34	0.27±0.28	2.96±0.89	6.76±0.91	1.57±0.58	45.18±0.68
SAF-03	0.86±0.34	0.27±0.25	4.11±1.18	4.23±0.91	1.93±0.64	44.73±1.03

MLA-02	1.03±0.19	0.33±0.16	3.85±0.91	8.09±1.28	1.40±0.50	47.42±0.70
MLA-01	1.02±0.20	0.32±0.16	3.80±0.81	7.38±1.18	1.37±0.41	47.78±0.62
LAM-07	0.61±0.26	0.12±0.21	2.24±0.73	4.34±0.65	1.30±0.59	47.58±0.60
LAM-06	0.64±0.25	0.07±0.14	2.02±0.93	1.70±0.56	1.42±0.50	45.88±0.58

Branches

SAF-01	0.21±0.30	0.12±0.22	2.58±1.00	4.03±1.32	0.63±0.55	47.45±1.34
SAF-02	0.16±0.24	0.09±0.16	2.19±0.71	2.88±0.79	0.51±0.40	46.20±0.56
SAF-05	0.27±0.30	0.33±0.39	3.67±1.18	2.93±1.20	0.69±0.54	45.64±0.72
SAF-04	0.19±0.29	0.10±0.14	2.16±0.81	2.94±0.90	0.41±0.41	46.55±0.60
SAF-03	0.25±0.33	0.12±0.19	2.32±0.89	2.52±0.96	0.75±0.61	46.36±0.90
MLA-02	0.36±0.55	0.11±0.24	1.62±0.82	1.90±0.81	0.40±0.21	46.94±0.81
MLA-01	0.34±0.54	0.10±0.25	1.52±0.93	1.73±0.80	0.36±0.19	47.23±0.85
LAM-07	0.19±0.25	0.07±0.25	0.97±0.38	1.70±0.75	0.34±0.21	46.42±0.52

LAM-06	0.17±0.16	0.04±0.09	0.79±0.45	1.10±0.52	0.51±0.34	45.72±0.63

Fine roots

SAF-01	0.84±0.46	0.35±0.19	4.88±0.96	4.98±0.92	1.43±0.48	43.29±1.09
SAF-02	0.89±0.36	0.39±0.15	4.61±1.00	4.20±0.98	1.37±0.40	44.09±1.03
SAF-05	0.86±0.44	0.56±0.29	6.34±0.84	6.82±0.97	2.16±0.57	42.09±1.13
SAF-04	0.84±0.51	0.35±0.20	4.92±0.97	4.76±0.86	1.43±0.70	43.49±1.03
SAF-03	0.88±0.45	0.35±0.20	4.76±1.02	2.86±0.82	1.35±0.54	43.89±1.37
MLA-02	0.60±0.30	0.27±0.22	4.66±0.79	4.36±1.19	0.92±0.57	44.28±0.70
MLA-01	0.68±0.28	0.28±0.22	4.68±0.86	3.30±0.93	0.82±0.47	44.48±0.57
LAM-07	0.69±0.13	0.26±0.14	4.26±0.66	1.64±0.56	1.65±0.71	44.11±0.60
LAM-06	0.67±0.29	0.23±0.26	4.26±1.41	0.72±0.50	1.41±0.72	47.13±0.94

Table S5.2. Soil characteristics of the study plots. Weighted mean concentrations of total C, N, P, K Ca, Mg, effective cation exchange capacity (eCEC), pH (H_2O), sand and clay ratio by subsoil layer depth from 30 cm up to 300 cm.

Plot code	C (%)	N (%)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	eCEC (mmol+/kg)	pH	Sand (%)	Silt (%)	Clay (%)
SAF-01	0.30	0.049	270.09	99.00	27.39	43.18	53.88	4.95	52.45	36.82	10.74
SAF-02	0.16	0.038	331.09	115.17	366.84	291.43	70.84	5.44	40.24	45.90	13.85
SAF-05	3.97	0.317	408.99	45.79	245.20	468.07	57.21	5.74	13.37	56.75	29.87
SAF-04	0.56	0.116	122.36	34.84	13.54	30.31	42.22	4.47	59.84	34.98	5.19
SAF-03	0.41	0.105	75.05	49.48	16.48	11.68	27.49	4.74	67.56	22.33	10.10
MLA-02	1.35	0.181	163.82	55.70	4.86	9.30	50.93	4.89	43.62	37.37	19.02
MLA-01	0.29	0.069	118.34	80.07	6.15	41.69	55.17	5.03	43.46	37.44	19.10
LAM-07	0.29	0.047	NA	18.98	2.43	6.78	37.85	3.79	42.40	31.79	25.81
LAM-06	0.09	0.020	NA	24.62	1.44	1.88	16.53	4.81	68.68	16.06	15.26

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Chapter 6, Overview

The previous chapter focused on the quantification of the nutrient budgets and the effect of logging disturbance on these budgets. In this chapter, I use the same dataset but shift the focus to the relationships between ecosystem nutrient budget, net primary productivity and soil nutrient content. I explore whether there is evidence of limitation for each nutrient and if so, what kind of ecosystem strategies, such as nutrient resorption of shifting stoichiometry, are invoked under limitation.

I conceived the study together with my supervisors and led on the analyses and writing. I collected all the data on the nutrient stoichiometry. Terhi Riutta and Kho Lip Khoon collected the net primary productivity data. Noreen Majalap-Lee led the chemical analyses. Reuben Nilus helped with the species identification and fieldwork logistics.

Chapter 6 Soil nutrient status does not predict tropical forest productivity because of contrasting nutrient strategies: novel insights from a whole ecosystem nutrient budget approach

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Abstract

Soil nutrients such as phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) are thought to be limited in supply in tropical forests. However, there have been very few direct studies of nutrient uptake and nutrient use efficiency in tropical forests, and their relationship to soil nutrient availability. Here we report on the relationship between net primary productivity (NPP), nutrient uptake and resorption across nine old-growth and logged lowland wet tropical forests in Sabah, Malaysian Borneo.

Contrary to expectation, NPP did not correlate with soil nutrient availability of any elements, suggesting soil availability is a weak predictor of NPP. We examined the

reasons for this by examining the vegetation biogeochemical cycles of five key macro- and micronutrients (N, P, K, Ca, Mg). For N and Mg, we found very little evidence of limitation: uptake rates showed no relationship with soil nutrient status across all sites, and there was no evidence of ecosystem strategies such as increased leaf nutrient resorption or shifting stoichiometry when uptake rates were lower. The remaining three nutrients showed evidence of shifting strategies under limitation, with clear evidence for thresholds below which compensation strategies were invoked, and contrasting strategies employed for each nutrient. For K, there was no shift in stoichiometry and enhanced leaf resorption was the primary strategy. For Ca, leaf resorption was not possible and shifting stoichiometry was the primary strategy. For P, a combination of both enhanced resorption and shifting stoichiometry was invoked. The strongest relationships were found for P and K, with old-growth forests showing some limitation and logged forests having sufficient supply. This employment of multiple nutrient compensation strategies explains why the relationship between soil nutrient status and ecosystem productivity is not linear or straightforward.

Key words: carbon cycling; ecophysiology; Malaysian Borneo; net primary productivity; NPP; nutrient cycling; nutrient uptake; nutrient resorption; tropical forest

Chapter 6

INTRODUCTION

The availability of one or more soil nutrients such as phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) is considered to limit the productivity in tropical forests, where highly weathered soils are depleted in these rock-derived nutrients (Tanner et al., 1998, Wright et al., 2011). Nitrogen (N), on the other hand, is not considered limiting in most old-growth tropical forests, although it may be limiting in secondary forests or at dry times of the year (Davidson et al., 2007). Particularly in highly weathered soils in lowland tropical forests, soil texture plays a key role in belowground C storage, nutrient availability and retention (Silver et al., 2000). Clay soils tend to have higher net primary productivity (NPP), cation exchange capacity, and litter decomposition rates (Uehara, 1995), while sandy soils are often associated with high fine root biomass due to larger C allocation to roots for nutrient and water capture (Cuevas and Medina, 1988).

It is widely suggested that in tropical forests tree growth and NPP are mainly constrained by soil P availability (Sollins, 1998, Tiessen, 1998, Cleveland et al., 2002). Much of the evidence is correlational: a meta-analysis by Cleveland et al. (2011) reports that P availability regulates NPP and other ecosystem processes in lowland tropical forests. In Amazonia, NPP strongly correlates with soil and foliar P concentrations (Porder et al., 2007, Vitousek et al., 2010). In West Kalimantan, aboveground NPP strongly correlates with soil P and P uptake (Paoli et al., 2005). In addition, soil P appears the primary driver of spatial patterns of NPP in Bornean

tropical forests (Paoli and Curran, 2007). The deficiency of P results in long-term reductions of C storage capacity due to slow P supply through deposition and lack of other external sources (Herbert et al., 2003). The impact of P limitation on tropical plant ecophysiology and forest ecology, however, is yet poorly studied both at the individual and plant community-level (Dalling et al., 2016). The expectation is that NPP is highly constrained by P availability, and it can be reasonably predicted from P content, namely soil P and P uptake. In contrast, the limitation of other elements is likely to show plot-specific variation, therefore NPP may not be predicted along the soil availability gradient of a single element of either N, K, Ca or Mg.

Although edaphic factors may appear to be primary drivers for NPP, low soil availability is counterbalanced by nutrient conservation mechanisms such as intensive acquisition (Comerford, 2005), efficient internal use (Paoli et al., 2005), and large resorption from senescent leaves (Kobe et al., 2005). The relative role of these various processes in compensating for limited nutrient supply is poorly quantified.

Firstly, in nutrient limited soils, plants may increase nutrient uptake by enhancing root exploitation of topsoil rather than improving absorption rate per root surface unit (Chapin, 1980). The ability of nutrient uptake can be directly measured, for example, by tracer experiments (Lehmann and Muraoka, 2001, Lehmann et al., 2001). Available techniques for assessing nutrient uptake at the root surface is discussed in Lucash et al. (2007).

Secondly, plants on less fertile soils use nutrients more efficiently as indicated by less nutrient return from litterfall to soil (Cuevas and Medina, 1986, Silver, 1994). Nutrient use efficiency is estimated as the ratio of biomass production to nutrient uptake (Hirose, 1975), i.e. total NPP per nutrient uptake (Bridgham et al., 1995). It can be measured at leaf, plant or ecosystem scale (Grubb, 1989, Ewel and Hiremath, 1998). Nutrient use efficiency is a key concept for understanding how resource availability determines spatial patterns of NPP (Chapin, 1980, Vitousek, 1982). High P use efficiency may indicate P limitation to NPP, in other words, less P efficient forests can be found in soils rich in available P (Vitousek, 1982, Silver, 1994). Such flexibility in tissue concentration may indicate that non-essential uses of P (such as storage in vacuoles) are restricted, while essential metabolic uses of P are still maintained. Such high P use efficiency is derived from increased retention time of P in biomass and decreased tissue P concentration (Dalling et al., 2016). An increase in photosynthetic P use efficiency with decreasing soil P is documented in montane forests in Borneo (Hidaka and Kitayama, 2009), and a study in West Kalimantan demonstrates that P use efficiency increases with declining soil P (Paoli et al., 2005).

Previous studies in tropical forests have focused either on the nutrient use efficiency of fine litter production (Silver, 1994, Kitayama et al., 2000) or of photosynthetic leaves (Hidaka and Kitayama, 2009, 2013), but comprehensive studies on whole-plant use efficiency are scarce (e.g., Hiremath et al., 2002, Paoli et al., 2005). In addition to use efficiency, the proportion of available soil nutrients acquired by plants is defined as nutrient uptake efficiency (Bridgham et al., 1995). This study will take a plant

community-level approach to assess total use efficiency and uptake efficiency (in this case, at plot-level).

Thirdly, while plants have evolved to optimise nutrient uptake and growth, they have another strategy to reduce nutrient losses by nutrient resorption, in which plants withdraw mobile nutrient elements from senescing leaves before abscission. In other words, it is a functional disconnection in foliage that stays attached to the plants, which enables them to minimise the loss of growth-constraining nutrients and to be less dependent on nutrient uptake from the soil (Eckstein et al., 1999, van Heerwaarden et al., 2003). From the leaf economic perspective, P resorption is assumed to be higher in P-limited tropical soils (Vitousek, 1984, Aerts, 1997b, Aerts and Chapin, 1999), although such relationship may vary due to strong heterogeneity in tropical soils (Richter and Babbar, 1991).

To date, there have been no studies that have assessed total nutrient requirement of tropical forest ecosystems and how this requirement is allocated amongst diverse organs. One approach to assess this is to couple measurements of NPP with measurement of the stoichiometry of live and senescent plant organs. Here, we use this approach to understand and quantify the relationship between NPP and nutrient uptake, requirement and resorption in contrasting intact and logged tropical forests in Borneo.

Our overall aim is to examine **the relationships between ecosystem nutrient**

budgets and net primary productivity in contrasting forests in Malaysian Borneo. We address the following research questions and hypotheses:

Q1) How does NPP vary with soil nutrient content in intact and logged tropical rainforests?

We hypothesise that NPP can be predicted from soil nutrient concentrations of rock-weathered nutrients, in particular phosphorus, at least in undisturbed forests with no dry season.

Q2) How does nutrient uptake rate vary with soil nutrient content?

We hypothesise that nutrient uptake rates increase linearly with soil nutrient content for all nutrients.

Q3) How does the contribution of resorption to nutrient requirement vary with nutrient uptake rate?

We hypothesise that the contribution of nutrient resorption increases linearly with decreasing soil nutrient uptake rates.

Q4) How does nutrient use efficiency vary with nutrient uptake rate?

We hypothesise that the stoichiometry (use efficiency) of some nutrients shifts when uptake rates are low, but that other nutrients are inflexible in their stoichiometry.

Q5) Can allocation shifts to wood explain how NPP is maintained in nutrient-poor

sites?

If there is increased production of low nutrient content tissue (wood) in sites with low nutrient uptake rates, this would be a mechanism to maintain high NPP under low nutrient conditions.

MATERIALS AND METHODS

Plot descriptions:

The study was conducted in nine permanent intensive carbon plots located across the states of Sabah and Sarawak, Malaysian Borneo (Table 6.1). The plots are part of the Global Ecosystems Monitoring (GEM) network (see http://gem.tropicalforests.ox.ac.uk; Malhi et al., 2021). The vegetation type is a mixed dipterocarp lowland rainforest, which is the most extensive forest type in Malaysian Borneo. Five plots, located in Kalabakan Forest Reserve, Sabah, had been previously logged at different intensities (Ewers et al., 2011, Struebig et al., 2013), constituting a disturbance gradient from heavily to moderately logged forest plots (Riutta et al., 2018). Two old-growth forest plots were located in Maliau Basin Conservation Area, Tongot District, Sabah, and the other two in Lambir Hills National Park, Miri District, Sarawak. Neither old-growth forest area had any record of either logging or other structural disturbance. The Sabah plots are part of the Stability of Altered Forest Ecosystems (SAFE) Project, one of the world's largest experiments in human-modified forest landscapes (Ewers et al., 2011). All nine plots had a planimetric area of 1 ha, which

was divided into 25 subplots of 20 m × 20 m. A description of all the plots and their productivity is given in Riutta et al. (2018).

The study plots in Sarawak harbour the highest recorded tree species richness in the Paleotropics (Palmiotto et al., 2004, Ashton, 2005). In all plots, Euphorbiaceae and Dipterocarpaceae were the most species-rich families among trees >10 cm DBH, with the Dipterocarpaceae dominating in overall biomass. In the old-growth plots, the most common genera were the dipterocarp genera *Shorea* and *Parashorea* in Maliau, *Shorea* and *Dryobalanops* in Lambir, while in the logged plots the most common genera were *Macaranga* (Euphorbiaceae), *Shorea* (Diptocarpaceae) and *Syzygium* (Myrtaceae). See Kho et al. (2013), Riutta et al. (2018), and Both et al. (2019) for detailed description of the species composition.

Soils around the study plots in Sabah have developed over rocks of the Kuamut formation and are mainly orthic Acrisol or Ultisols, formulated on sandstone and mudstone (Burghouts, 1993). In the study plots in Sarawak, soils vary between sandstone-derived sandy loam humult Ultisols on ridges, and shale-derived clay of clay-rich udult Ultisols (Kho et al., 2013) in valleys. For soil nutrient contents see Table 6.2. The mean annual temperature and precipitation in the region are 26.7 ±1.9 °C and 2600-2700 mm (Walsh and Newbery, 1999, Kumagai et al., 2004, Kumagai and Porporato, 2012). Although no distinct seasonality exists in typical years, some drier months occur in most years, and ecologically significant droughts occur during El Niño events (Malhi and Wright, 2004). As there is no regular dry season at any of these

sites, this study controls for the effect of water stress on NPP, enabling us to isolate soil nutrient controls on NPP and nutrient cycling separate from water stress factors.

The short distance (typically a few km) between some plots could potentially raise issues of pseudoreplication (Malhi et al., 2015). However, the two adjacent plots both in Maliau and Lambir sites showed considerable differences in soil conditions and species composition, sufficient to treat them as independent sample points. In Lambir, one plot is on relatively fertile clay soil, while the other is on relatively infertile sandy soil (Table 6.2). Logged plots in close proximity can also be treated as independent due to high spatial heterogeneity in logging intensity. See also multivariate analyses in Riutta et al. (2018) and Both et al. (2019), showing that variation within forest types is larger than between forest types.

Table 6.1 Characteristics of the study plots

Plot code[a]	Plot location	Disturbance	Soil type; topography	Basal area of trees > 10 cm DBH (m^2 ha^{-1})[b]	Mean canopy gap fraction (%)[b]	Mean forest quality score[c]
SAF-01	SAFE Project Experimental Area (4.732°, 117.619°), Sabah	Heavily logged	Clay; mostly flat with a moderate slope on one edge	6.81 ± 1.00	15.0 ± 2.14	2.2
SAF-02	SAFE Project Experimental Area (4.739°, 117.617°), Sabah	Heavily logged	Clay; undulating	11.1 ± 1.81	13.4 ± 1.51	2.6
SAF-05	SAFE Project Experimental Area (4.716°, 117.609°), Sabah	Heavily / moderately logged	Clay; undulating	13.9 ± 1.70	12.2 ± 2.07	2.7
SAF-04	SAFE Project Logged Forest Area (4.765°, 117.700°), Sabah	Moderately logged	Mostly sandy loam, partly clay; flat	19.3 ± 1.70	12.8 ± 1.03	3.2

SAF-03	SAFE Project Experimental Area (4.691°, 117.588°), Sabah	Moderately logged	Clay; steep slope	19.6 ± 1.88	11.2 ± 1.29	3.2
MLA-02	Maliau Basin Conservation Area (4.754°, 116.950°), Sabah	Old-growth	Clay; moderate slope	34.7 ± 2.74	7.04 ± 0.55	5.0
MLA-01	Maliau Basin Conservation Area (4.747°, 117.700°), Sabah	Old-growth	Clay; undulating	41.6 ± 3.59	8.70 ± 0.62	5.0
LAM-07	Lambir Hills National Park (4°12'N, 114°2'E), Sarawak	Old-growth	Clay; undulating valley bottom	31.8 ± 3.85	10.5 ± 0.45	5.0
LAM-06	Lambir Hills National Park (4°12'N, 114°2'E), Sarawak	Old-growth	Sandy loam; undulating ridge top	41.1 ± 2.45	9.52 ± 0.22	5.0

[a]Plot code as in the ForestPlots database (ForestPlots.net)

[b]DBH – Diameter at breast height (1.3 m); Basal area and gap fraction denote the mean ± 1 SE of individual subplots.

[c]Individual 20 m × 20 m subplots within each 1 ha plot (*n* = 25) were subjectively ranked into the forest quality classes *a priori,* from 1 (heavily disturbed) to 5 (no signs of human disturbance), using the presence of stumps and felled trees, evidence of logging trails, number of large (≥ 30 cm DBH) trees and canopy closure as the assessment criteria.

Table 6.2 Soil characteristics of the study plots. Weighted mean (± 1 SE) concentrations of total C, N, P, K Ca, Mg, effective cation exchange capacity (eCEC), pH (H2O), sand and clay ratio by topsoil layer depth to 30 cm.

Plot code	C (%)	N (%)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	eCEC (mmol+/kg)	pH	Sand (%)	Silt (%)	Clay (%)
SAF-01	1.23	0.137	255.6	73.3	403.6	124.4	59.4	4.34	49.5	30.6	20.0
	±0.56	±0.05	±38.7	±9.6	±155.5	±44.8	±3.2	±0.08			
SAF-02	0.63	0.064	115.6	84.3	70.0	42.3	51.1	4.26	44.5	36.0	19.5
	±0.38	±0.03	±4.2	±18.2	±0.90	±15.1	±2.2	±0.19			
SAF-05	1.87	0.196	366.4	49.1	398.0	314.7	54.7	4.85	20.8	51.7	27.5
	±0.33	±0.04	±42.5	±1.4	±134.0	±50.8	±4.8	±0.25			
SAF-04	2.96	0.178	66.5	30.1	35.6	17.6	6.2	4.14	46.2	31.5	22.3

	±0.97	±0.02	±4.5	±7.3	±12.8	±2.9	±1.7	±0.57			
SAF-03	0.98	0.104	150.0	79.6	28.0	20.8	32.7	3.80	65.6	24.9	9.5
	±0.43	±0.01	±20.0	±25.2	±3.4	±25.2	±6.3	±0.18			
MLA-02	1.02	0.126	199.2	67.4	90.4	87.7	46.4	4.26	35.7	44.4	19.9
	±0.22	±0.02	±11.1	±13.6	±34.6	±57.6	±2.3	±0.29			
MLA-01	0.80	0.084	141.4	71.1	22.6	30.6	44.9	3.99	43.5	33.9	22.6
	±0.25	±0.01	±15.8	±7.6	±6.7	±7.47	±7.0	±0.08			
LAM-07	0.95	0.098	126.9	61.9	68.0	89.2	36.0	4.49	45.6	42.7	11.7
	±0.07	±0.02	±NA	±21.3	±5.77	±46.7	±6.9	±0.16			
LAM-06	1.16	0.089	73.4	42.5	4.1	9.2	30.4	4.38	69.1	19.2	11.8
	±0.08	±0.01	±NA	±10.4	±2.2	±4.4	±9.1	±0.03			

Sampling of tree components:

Nutrient samples were collected between January and March in 2014. We selected 15 trees (≥ 10 cm diameter at breast height [DBH]), consisting of five tree species with three replicates each (*n* = 15) outside, but within 100 m of the plot boundary of each plot, representing the most common species of the plot (see Table S6.2). Sampled trees had no visible damage (e.g. no insect damage, chlorotic leaves, bent stems). Four tree components were collected from each tree: branches, green leaves, senesced leaves and fine roots. The total number of samples was 540 (5 trees species × 3 replicates × 4 components × 9 plots). Collected voucher specimens of chosen trees were identified at the species level at the herbarium of the Forest Research Centre in Sabah, Malaysia.

Mature branches with fully expanded green leaves were obtained using a long pole with a saw blade, by tugging a rope cast over a branch with a fishing rod, or by climbing. Although the collection of sun leaves is often recommended by functional trait protocols for foliar nutrient analysis (Cornelissen et al., 2003), we collected shade leaves because the majority of trees and leaves (≥ 10 cm DBH) were shaded, particularly in old-growth plots. It was also to ensure a consistency in the leaf sampling across plots, and to match green leaves against freshly fallen senesced leaves for leaf resorption estimation assuming that the majority of fallen leaves were shade leaves. The selection of sun and shade leaves is unlikely to be influential. A study of 32 leaf traits across 284 species in Borneo, where the data were collected partly from the

same plots as this study, found no systematic differences between sun and shade leaves (Both et al., 2019). Similarly, an analysis of leaf plasticity to light showed that the species ranking in mean concentrations of N and P was maintained across sun and shade leaves for 38 tropical tree species in Bolivia (Rozendaal et al., 2006). All sampled branches were ≥ 1 cm in diameter and were dissected into disks. The disks were taken in the midpoint of the branch (i.e. not near the trunk nor the tip of the branch). Newly shed senesced leaves were collected from the ground; all such collected leaves were intact, fully brown and identical in shape and size to the green leaves. Twenty green and senesced leaves from each individual tree were collected for chemical analysis, and were pooled, resulting in one sample of green leaves, and one sample of senesced leaves per tree.

Mature living fine roots (here defined as roots of ≤ 5mm in diameter) were excavated near to the coarse root of each sampled tree. They were sieved and washed with tap water. These samples contained not only fine roots of the target tree but also possibly of other plants as they were not able to be distinguished empirically. We, therefore, treated them as plot-level (i.e. plant community level) samples, not as individual tree samples in our study. Fine roots were, therefore, analysed for two replicates per species per plot only (n = 10 per plot).

A tree census was conducted, and 425 species (≥ 10 cm DBH) from 175 genera were identified from 2,155 trees across five logged forest plots. The species sampled for this study accounted for, on average, 26%, 41% and 53% of the species, genus and

family basal areas, respectively, in the logged plots. This enabled us to cover a broad taxonomic and functional type range from light-demanding pioneer to shade-tolerant late-successional species.

In the two old-growth forest plots in Maliau, the total number of stems, 882, comprised 239 species from 118 genera. In the two old-growth forest plots in Lambir, the total number of stems, 809, comprised 360 species representing 118 genera. The species sampled for this study accounted for, on average, 16%, 37% and 65% of the species, genus and family basal areas, respectively, in the old-growth plots.

Plot-level values were estimated from the species-level data by a nested weighting approach: first, each species was assigned the weight of its basal area proportion. Then, unsampled species within the same genus were assigned a genus-level mean, and finally unsampled species within the same families were assigned a family-level mean. We only weighted according to sampled families – unsampled families were ignited in calculating plot-level weighted mean concentrations. To increase the proportion of the sampled species in each plot, we combined species-level estimates from the plots of the same area and disturbance class, that is, we combined species-level data among logged plots, and among the two old-growth plots in Maliau. We did not combine the species-level data in the two old-growth plots in Lambir due to their strongly contrasting soil types.

Chemical analyses of plant tissues:

Concentrations of five macronutrient elements (N, P, K, Ca and Mg) and carbon (C) in each individual component were quantified at the chemistry laboratory in Forest Research Centre, in Sabah, Malaysia. First, all samples were oven dried at 50°C to constant weight for five days, and were then ground with a Thomas Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to pass through a 100-mesh (212-μm) sieve. Branch samples including the bark were chipped to small pieces before grinding. Both green and senesced leaves included petioles.

Most of the protocols are described in Majalap and Chu (1992). Summary of the methods used are as follows. Each sample was digested following the sulphuric acid-hydrogen peroxide-lithium sulphate digest procedure for vegetation described in Allen (1989). Phosphorus in the digest was determined using the molybdenum-blue method described in Anderson and Ingram (1993) and read at 880 nm on a spectrophotometer (HITACHI UV-VIS, Tokyo, Japan), while K, Ca and Mg contents were measured on an atomic absorption spectrophotometer (GBC Scientific Equipment, Victoria, Australia). Total C and N contents (as total element contents) were determined by a dry combustion method at 900 °C using an Elementar Vario Max CN analyzer (Elementar Analysensysteme, Hanau, Germany).

Soil sampling and analysis:

Within each 1 ha plot, two soil cores to the depth of 100 cm were collected and divided into six depth layers (0-5, 5-10, 10-20, 20-30, 30-50, 50-100 cm), and one soil pit dug up to 300 cm, and samples collected from 10 layers divided into 10 depth layers (0-5,

5-10, 10-20, 20-30, 30-50, 50-100, 100-150, 150-200, 200-250, 250-300 cm) on the pit walls. We then defined the depth of 0-30 cm as topsoil layer (Table 6.2), and 30-300 cm as subsoil layer (Table S6.1). We used the topsoil layer as a proxy for soil nutrient availability in this study, where fine roots were mostly limited to the top 30 cm of soil profile (Yoda, 1978). Soil sampling was done following the standard RAINFOR protocol (see http://www.rainfor.org/en/manuals; Quesada et al., 2010) and soil samples were air dried in the field. Following the removal of roots, detritus, small rocks and particles over 2 mm, samples were then sieved at 2 mm, and analysed for: total P (modified from Hedley et al., 1982), and C and N (Pella, 1990, Nelson and Sommers, 1996), exchangeable cations by the silver-thiourea method (Pleysier and Juo, 1980), and pH in water at 1:2.5, along with bulk density, and soil texture (the proportion of sand, silt and clay) at the University of Leeds, United Kingdom.

Estimation of NPP

Net primary productivity (NPP) is the rate of biomass synthesis that is used to form organic compounds in plants (Roy and Saugier, 2001). It is expressed as the difference between gross primary productivity (GPP) (i.e. total ecosystem photosynthesis) and autotrophic respiration, and can be quantified at the scale of an individual plant or ecosystem (Malhi et al., 2011). The following NPP components were quantified: canopy (leaves, twigs, reproductive parts), woody (stem, coarse roots and branch), and fine roots. NPP data for seven plots in Sabah was collected during 2012 to 2014, over a 24 month period in each plot, and are described in detail in Riutta et al. (2018), while the data for two plots in Sarawak was collected for 15 months between 2008 and 2010, and tree census was carried out every five years during 1992 to 2008

(Kho et al., 2013). The data were collected using standardized GEM protocols (Marthews et al., 2014, Malhi et al., 2021). Methods are described in detail in a manual available on the GEM website (http://gem.tropicalforests.ox.ac.uk, and in the site-specific papers (Kho et al., 2013, Riutta et al., 2018).

Estimation of leaf nutrient and C resorption rate:

During senescence substantial leaf mass loss occurs, mainly due to the resorption of nutrients and C (Vergutz et al., 2012); thus, disregarding mass loss leads to an underestimation of resorption by ~10% (van Heerwaarden et al., 2003). Calcium has been reported not to be resorbed due to its immobility (Vitousek and Sanford, 1986, Lambers et al., 1998). A global meta-analysis by (Vergutz et al., 2012) documented that Ca resorption was statistically indistinguishable from 0% resorption for all woody species. We thus adopted the approach depicted in Vitousek and Sanford (1986): senesced leaf nutrient content was corrected with the mass loss correction factor (MLCF), using Ca content as a reference value. Measured nutrient concentration was multiplied by the ratio of Ca concentration in green leaves and in senesced leaves averaged over the plot total leaf set.

Our mean leaf mass loss derived from the mean green to senesced leaf Ca ratio was 25.0±3.5%, which was slightly higher than the mean leaf mass loss of tropical evergreen woody angiosperms of 22.6% averaged from 31 global data points (Vergutz et al., 2012), which did not include any observations from Bornean forests.

Nutrient (x) resorption rate (%) was computed for each sample as

$$R_x = \left(1 - \frac{x_{senesced}}{x_{green}} MLCF\right) \times 100$$

(Eq. 1)

where *x* is an element of either N, P, K, Ca, Mg or C, R_x is the resorption rate of *x*, x_{green} is *x* concentration in green leaves, $x_{senesced}$ is *x* concentration in senesced leaves, and MLCF is the green to senesced leaf Ca ratio. The MLCF was calculated separately for each species in each plot, and the mean MLCF was 0.75±0.035 across plots.

Estimation of nutrient stoichiometry, uptake, requirement and use efficiency:

x stoichiometry was expressed as C:*x* ratio, that is, the ratio of C concentration to *x* concentration of nutrient *x* in each plot.

The following set of equations were used to calculate total nutrient requirement, total uptake (= requirement – resorption), nutrient use efficiency (NPP divided by requirement), and nutrient uptake efficiency (NPP divided by uptake) for each nutrient and each site (Eq. 1-5):

$$xRequirement\ (kg\ x\ ha^{-1}\ year^{-1}) = \left[\left(\frac{NPP_{canopy}}{C{:}x_{green}}\right)\right] + \left(\frac{NPP_{wood}}{C{:}x_{wood}}\right) + \left(\frac{NPP_{fine\ roots}}{C{:}x_{fine\ roots}}\right)$$

(Eq. 2)

II. *Canopy* II: *Woody* III: *Fine roots*

$$xUptake\ (kg\ x\ ha^{-1}\ year^{-1})$$
$$= \left[\left(\frac{NPP_{canopy}}{C{:}x_{green}}\right) \times (1\ - R_x)\right] + \left(\frac{NPP_{wood}}{C{:}x_{wood}}\right) + \left(\frac{NPP_{fine\ roots}}{C{:}x_{fine\ roots}}\right)$$

(Eq. 3)

I. *Canopy uptake* II: *Woody uptake* III: *Fine root uptake*

$$xUse\ Efficiencies\ (kg\ C\ per\ kg\ x\ ha^{-1}\ year^{-1})$$
$$= \frac{NPP_{green} + NPP_{wood} + NPP_{fine\ roots}}{xRequirement}$$

(Eq. 4)

$$xUptake\ Efficiencies\ (kg\ C\ per\ kg\ x\ ha^{-1}\ year^{-1})$$
$$= \frac{NPP_{green} + NPP_{wood} + NPP_{fine\ roots}}{xUptake}$$

(Eq. 5)

The above estimations depend on the assumption that nutrients used for NPP are offset by an equivalent amount of nutrients accrued from soil (and nutrient resorption) over the annual cycle. Nutrient use or requirement is the total stoichiometric requirement to build plant tissue, and nutrient uptake is the fraction of that demand that is not met through resorption and hence requires fresh uptake from soil or litter. This calculation assumed negligible resorption during the fine root senescence, or during conversion of live wood to heartwood, as very little is known about those two processes (see Chapter 4 for the analysis of wood resorption).

The NPP_{wood} was the sum of stem, branch, and coarse root production, while $C{:}x_{wood}$ was estimated solely using the branch C and *x* content. To reduce a systematic bias towards either underestimation or overestimation because C and *x* contents in wood differed in different parts of a whole tree, the correction factors of 0.792 (N), 0.796 (P), 0.847 (K), 1.531 (Ca), 1.226 (Mg) and 1.007 (C) were applied to C:*x* wood. These correction factors were derived by taking the mean of C and *x* content of all other woody components (sapwood at the bottom of the trunk, heartwood at bottom of the trunk, sapwood at the middle height of the trunk, heartwood at the middle height of the trunk, and coarse roots) except branches, and dividing this mean by the branch content (see Chapter 4 for the analysis of wood nutrient allocation).

Nutrient uptake can be considered as the sum of nutrient accrual in above- and belowground biomass, nutrient returns to the soil via litterfall, and foliar leaching from the canopy. Hiremath et al. (2002) reported that foliar leaching N loss is < 0.5% of total N uptake and P loss is 1.7-10.9 % of total P uptake. Freschet et al. (2010) also documented leaching accounted for less than 1% of leaf N pool, and no more than 0.01% of the leaf P pool. The influence of leaching on leaf nutrient status appeared generally negligible compared with leaf resorption (Frangi et al., 2005, Vergutz et al., 2012). We therefore excluded the potential effect of leaching in our study.

Statistical analyses:

To address the research questions, we ran simple linear regression models, separately for each nutrient. To address Q1, we ran models with NPP as the response variable and the soil nutrient concentration as the explanatory variables. For Q2, we ran models with nutrient uptake from soil as the response variable and soil nutrient content as the explanatory variable. For Q3, we ran models with resorption contribution to total nutrient requirement as the response variable and nutrient uptake from soil as the explanatory variable. For Q4, we ran models with nutrient use efficiency as the response variable and nutrient uptake from soil as the explanatory variable. And finally, for Q5, we ran models with woody contribution to total nutrient requirement as the response variable and nutrient uptake from soil as the explanatory variable.

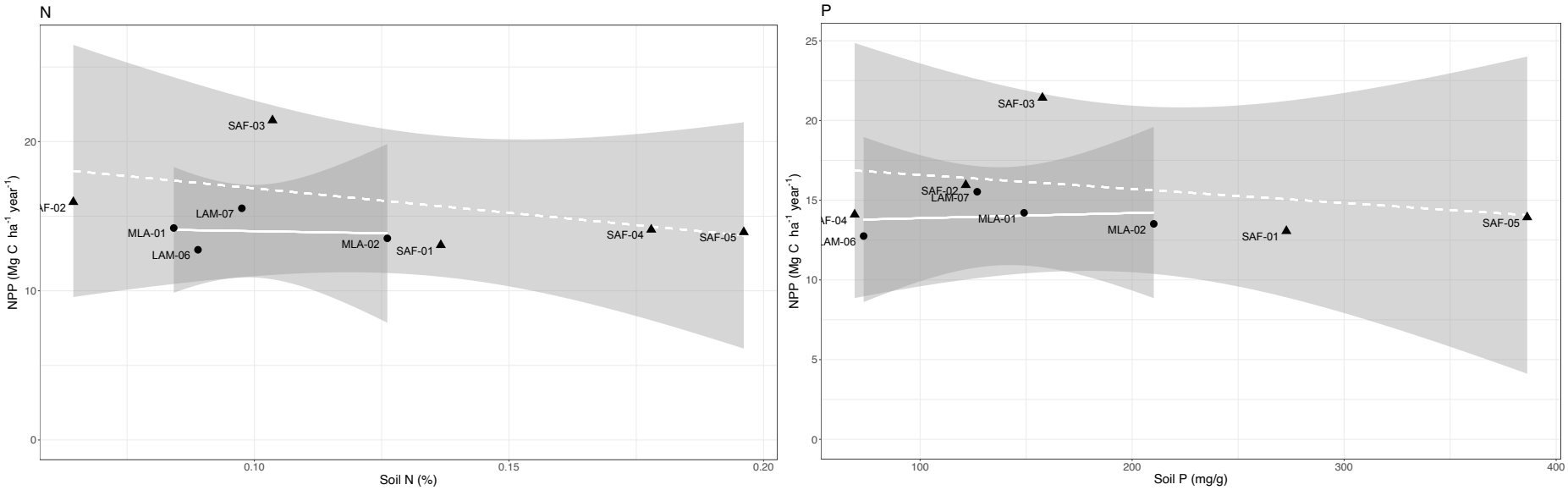
First, we applied the regression separately for logged and old-growth forests. Then, if there was evidence for a common pattern across the forest types, we ran the model for the full dataset, with and without an interaction with forest type. If the model results confirmed that the interaction with forest type was not significant (p-value > 0.05), we accepted this overall model. If there was evidence of a threshold phenomenon, we fitted a segmented regression for the full dataset. The significance of the segmented regression was assessed with Davies' test.

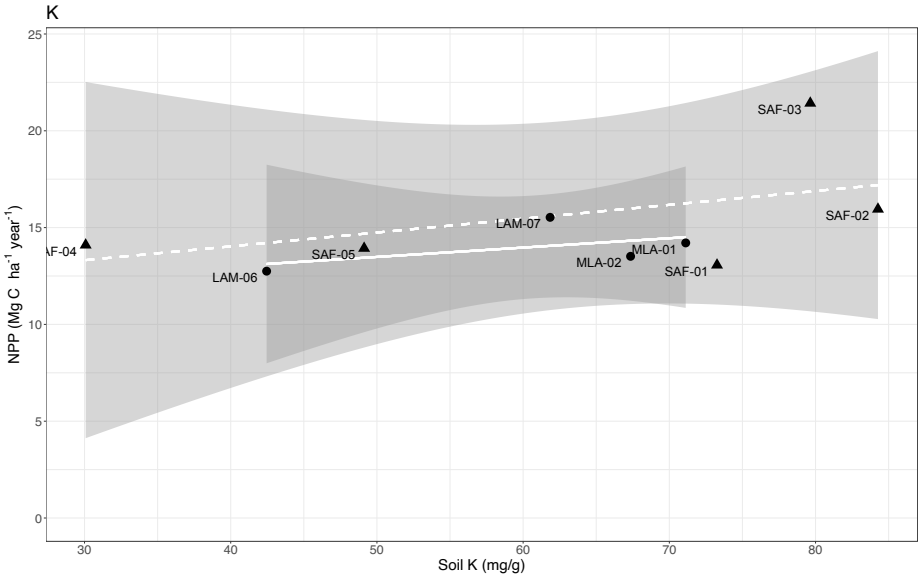
Statistical analyses were performed in the R programing language version 4.0.4 (R Core Team, 2021) and the packages 'ggplot2' (Wickham, 2016) and 'segmented' (Muggeo, 2003, Muggeo, 2008, Muggeo, 2016, Muggeo, 2017).

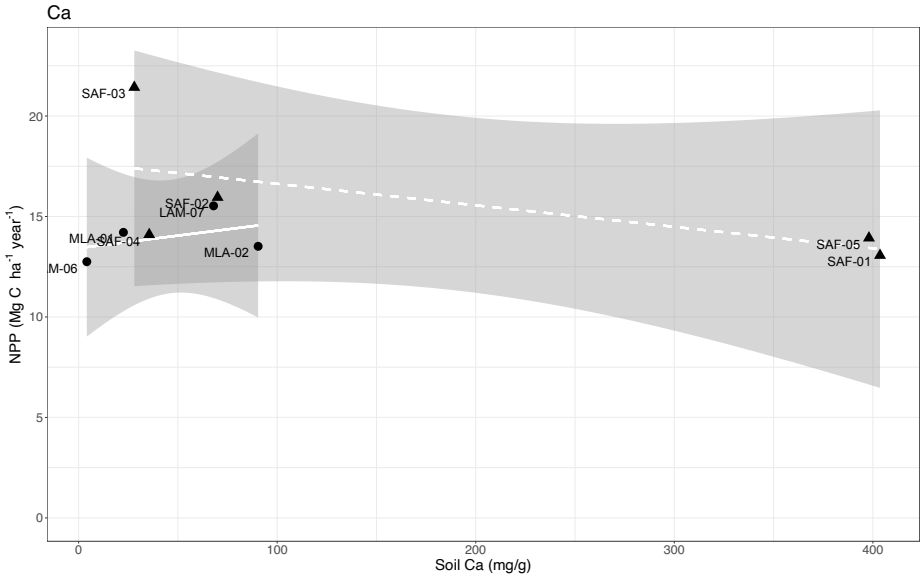
RESULTS

Q1) How does NPP vary with soil nutrient content in intact and logged tropical rainforests?

The relationships between soil nutrient concentrations of all elements and total NPP were surprisingly weak (Fig. 6.1), indicating that soil nutrient content is not a reliable predictor of NPP. This is true both within old-growth and logged forests, despite the overlap in soil P concentrations in the old growth and logged forests (Fig 6.2). The relationships between nutrient uptake from soil and total NPP were not significant either, except for N uptake and NPP in logged forests, which was mainly driven by one outlier (Fig. S6.1). Hence soil nutrient status has negligible predictive value in predicting NPP; we next examine exactly why this occurs.


N
NPP (Mg C ha-1 year-1)
Soil N (%)
SAF-03
LAM-07
MLA-01
LAM-06
MLA-02
SAF-01
SAF-04
SAF-05
P
Soil P (mg/g)
SAF-02
LAM-07
MLA-01
MLA-02
SAF-01
SAF-05


K
NPP (Mg C ha-1 year-1)
Soil K (mg/g)
SAF-03
SAF-02
LAM-07
SAF-05
MLA-01
MLA-02
SAF-01
LAM-06


Ca
NPP (Mg C ha-1 year-1)
Soil Ca (mg/g)
SAF-03
SAF-02
LAM-07
SAF-04
MLA-02
SAF-05
SAF-01

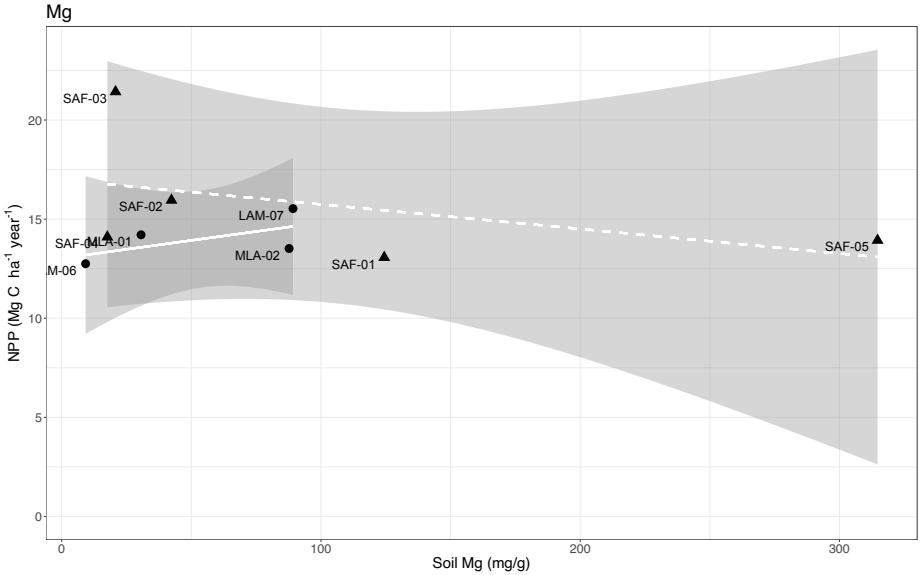
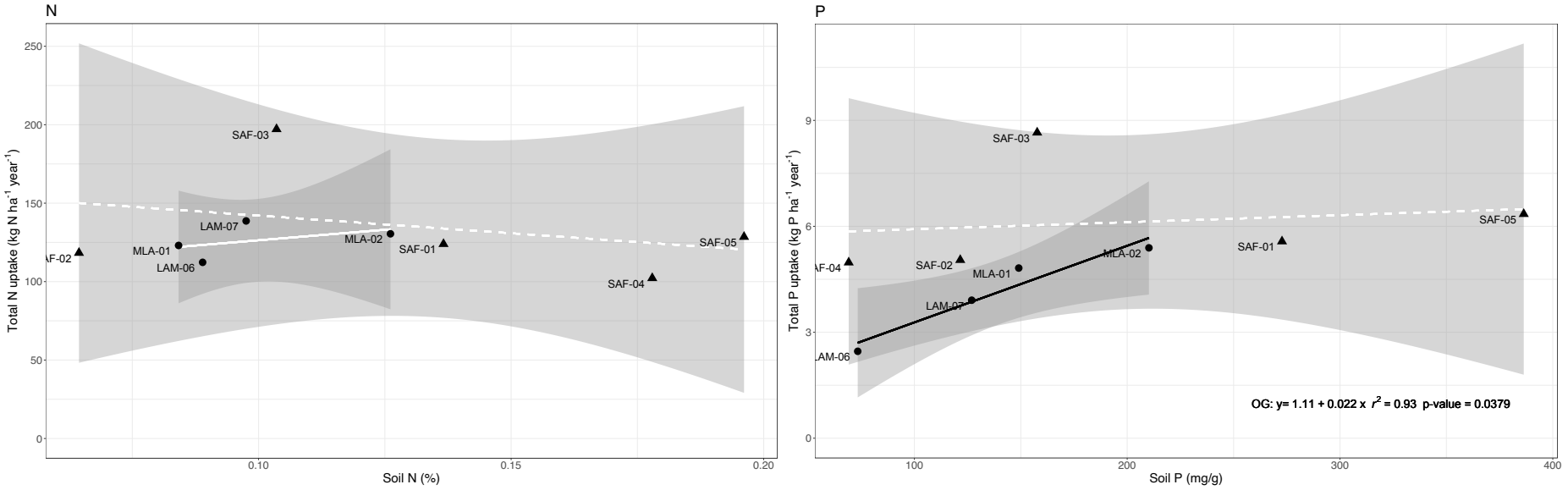
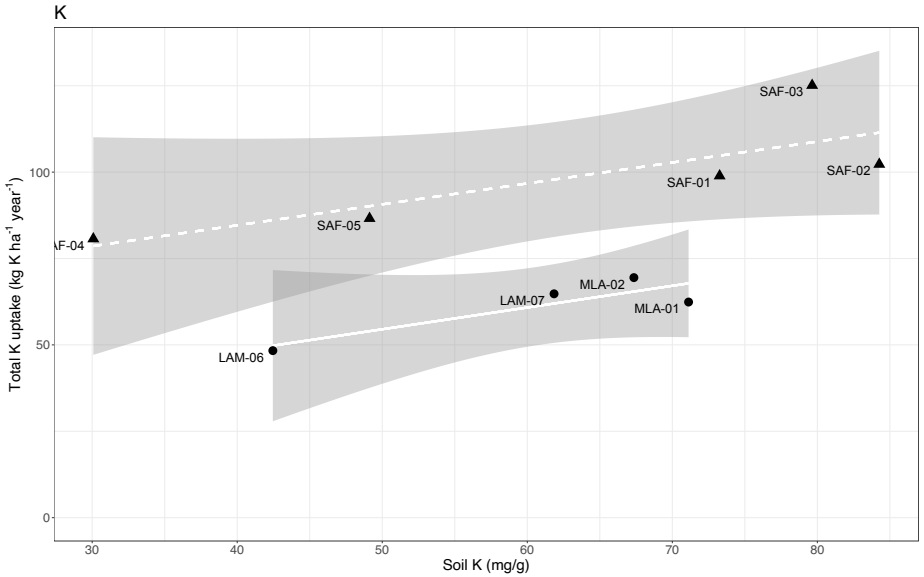
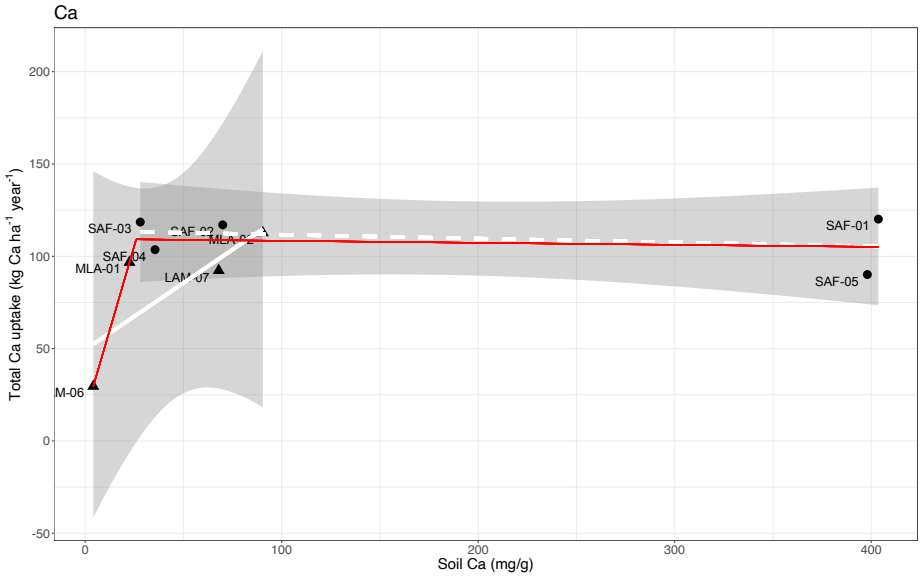

Mg
NPP (Mg C ha-1 year-1)
Soil Mg (mg/g)
SAF-03
SAF-02
LAM-07
MLA-01
MLA-02
SAF-01
SAF-05

Figure 6.1 Linear relationship, with confidence bands, of soil nutrient content and net primary productivity (NPP).

The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). None of the regressions were significant. The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (circles, MLA-02, MLA-01, LAM-07 and LAM-06) and logged (triangles, SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1.




K
Total K uptake (kg K ha-1 year-1)
Soil K (mg/g)
SAF-03
SAF-01
SAF-02
SAF-05
LAM-06
LAM-07
MLA-02
MLA-01


Ca
Total Ca uptake (kg Ca ha-1 year-1)
Soil Ca (mg/g)
SAF-03
SAF-01
SAF-05
MLA-01

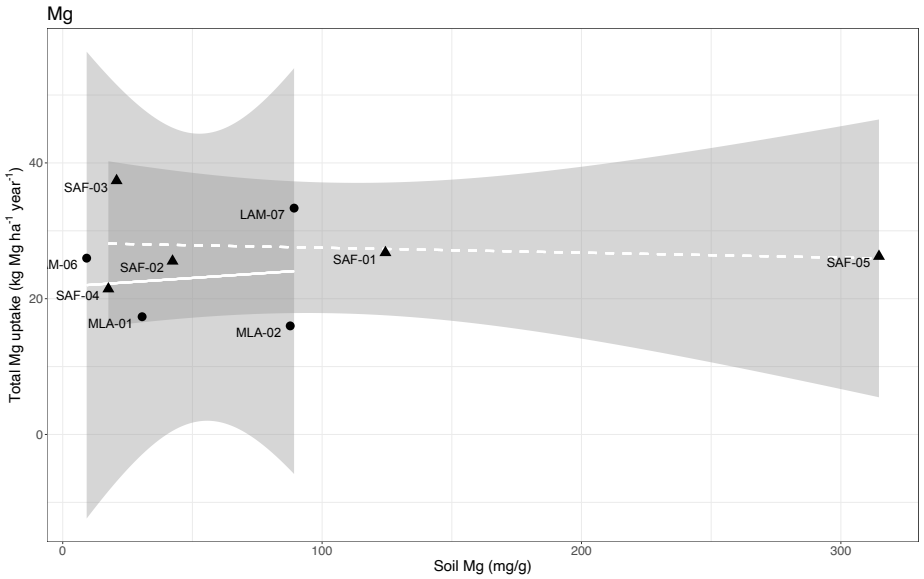

Mg
Total Mg uptake (kg Mg ha-1 year-1)
Soil Mg (mg/g)
SAF-03
LAM-07
SAF-02
SAF-01
SAF-05
SAF-04
MLA-01
MLA-02

Figure 6.2 Linear relationship, with confidence bands, of soil nutrient content and nutrient uptake.

The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). Significant lines by forest type are shown in black and non-significant lines in white. Regression equation is shown for significant regressions. The red line for Ca is a segmented regression fitted across forest types. The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (circles, MLA-02, MLA-01, LAM-07 and LAM-06) and logged (triangles, SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1.

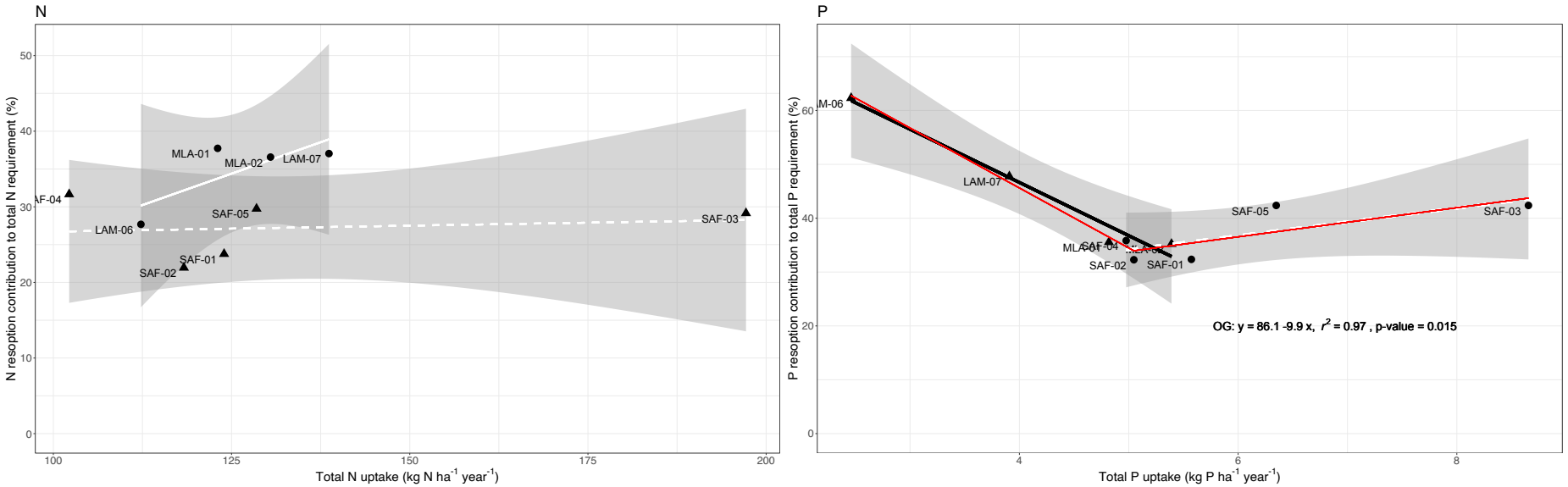
Q2) How does nutrient uptake rate vary with soil nutrient content

We found no significant relationships between nutrient uptake from soil and soil nutrient content for any of the elements except P (Fig. 6.2). For P, there was a significant positive relationship in old-growth forests but no relationship in logged forests. For K, there was a weak positive relationship in both forest types, with a similar slope but different intercepts in old-growth and logged forests. Ca uptake and soil Ca content in one of the old-growth plots (LAM-06) was exceptionally low. Other old-growth forests had similar Ca uptake rates as logged forests, irrespective of soil Ca. We found a evidence for a threshold at soil Ca content of 25.99±4.84 mg/g (p-

value of the Davies' test 0.014), but it is mainly driven by one single plot.

Q3) How does the contribution of resorption to nutrient requirement vary with nutrient uptake rate?

We now plot uptake rates as the x-axis, as a metric of soil availability and plant nutrient requirement.



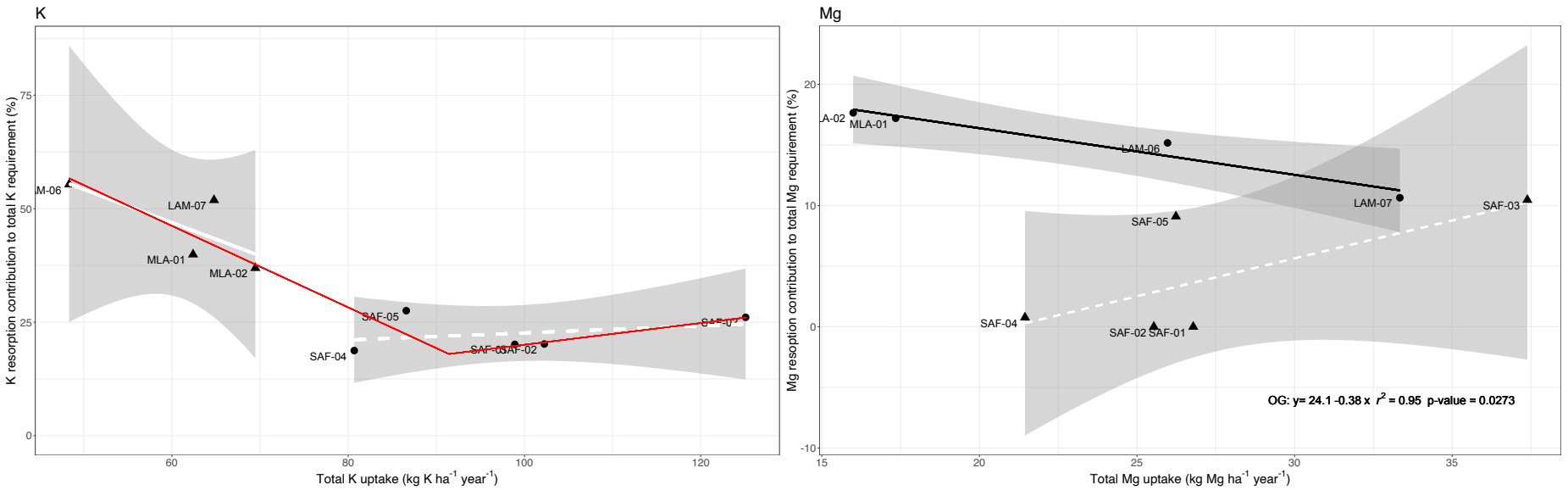


Figure 6.3 Linear relationship, with confidence bands, of total nutrient uptake and resorption contribution to nutrient requirement.

The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). Significant lines by forest type are shown in black and non-significant lines in white. Regression equation is shown for significant regressions. The red lines for P and K are segmented regressions fitted across forest types. The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (circles, MLA-02, MLA-01, LAM-07 and LAM-06) and logged (triangles, SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1. Note that Ca resorption was assumed to be zero, and was therefore excluded from this analysis.

For N, there were no significant relationships between resorption and uptake (Fig. 6.3). Furthermore, the slope in old-growth forests was non-significant but positive, opposite to what would be hypothesized (increased role for resorption when uptake is low).

For P, there was a very strong negative relationship for old-growth forests, and a weak, non-significant positive relationship for logged forests (Fig. 6.3). The two lines overlap at uptake rates of 5.05±0.20 kg P/ha/year, with both old-growth and logged forest points at this value. This suggests that a single threshold curve can explain this relationship ($p=0.001$). All logged forests were found at or above this threshold, and all old-growth forests were at or below this threshold.

For K, the pattern was similar to P, with a negative relationship for old-growth forests and flat relationship for logged forests, although the old-growth and logged forest regression lines did not intercept. The relationship, however, was not significant in either forest type. In combination, we found a significant ($p=0.033$) segmented regression across the forest types, this suggests a threshold uptake rate of 80.85±7.35 kg K/ha/year, below which resorption rates are enhanced.

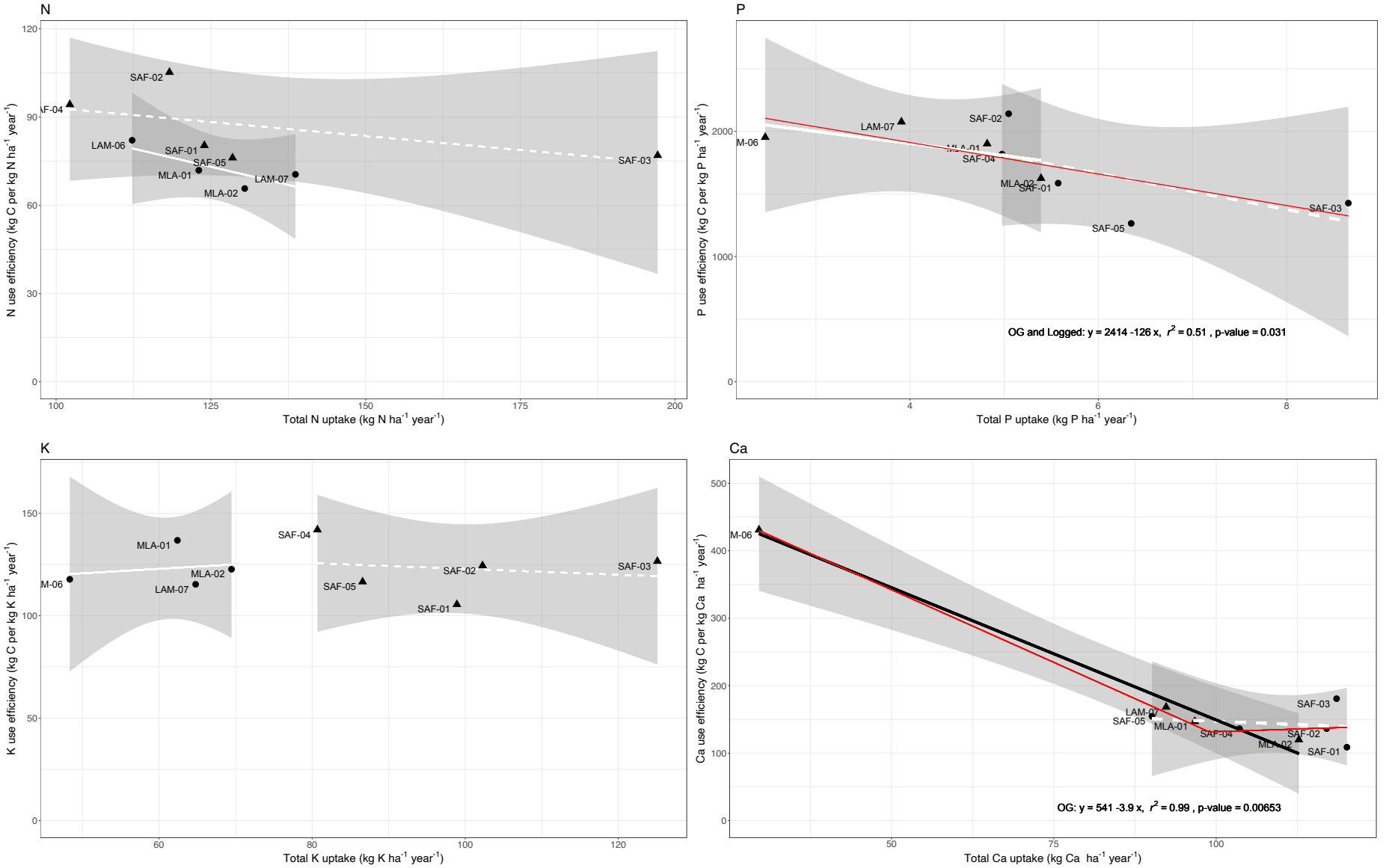
For Mg, there was a negative relationship for old-growth forests and a weak positive but non- significant relationship for logged forests

(Fig. 6.3). The uptake rates of the two forest types overlapped, but there was no overall pattern in the relationship across the forest types.

Calcium was not part of this analysis, as Ca resorption was assumed to be zero.

Q4) How does nutrient use efficiency vary with nutrient uptake rate?

We next examined how stoichiometry (nutrient use efficiency) varied with nutrient uptake rates.


N
N use efficiency (kg C per kg N ha-1 year-1)
Total N uptake (kg N ha-1 year-1)
SAF-02
SAF-04
LAM-06
SAF-01
SAF-05
MLA-01
LAM-07
MLA-02
SAF-03
P
P use efficiency (kg C per kg P ha-1 year-1)
Total P uptake (kg P ha-1 year-1)
LAM-07
SAF-02
M-06
SAF-04
MLA-02
SAF-01
SAF-05
SAF-03
OG and Logged: y = 2414 -126 x, r2 = 0.51 , p-value = 0.031
K
K use efficiency (kg C per kg K ha-1 year-1)
Total K uptake (kg K ha-1 year-1)
MLA-01
SAF-04
M-06
MLA-02
LAM-07
SAF-05
SAF-02
SAF-03
SAF-01
Ca
Ca use efficiency (kg C per kg Ca ha-1 year-1)
Total Ca uptake (kg Ca ha-1 year-1)
M-06
SAF-03
SAF-05
MLA-01
SAF-04
SAF-02
SAF-01
OG: y = 541 -3.9 x, r2 = 0.99 , p-value = 0.00653

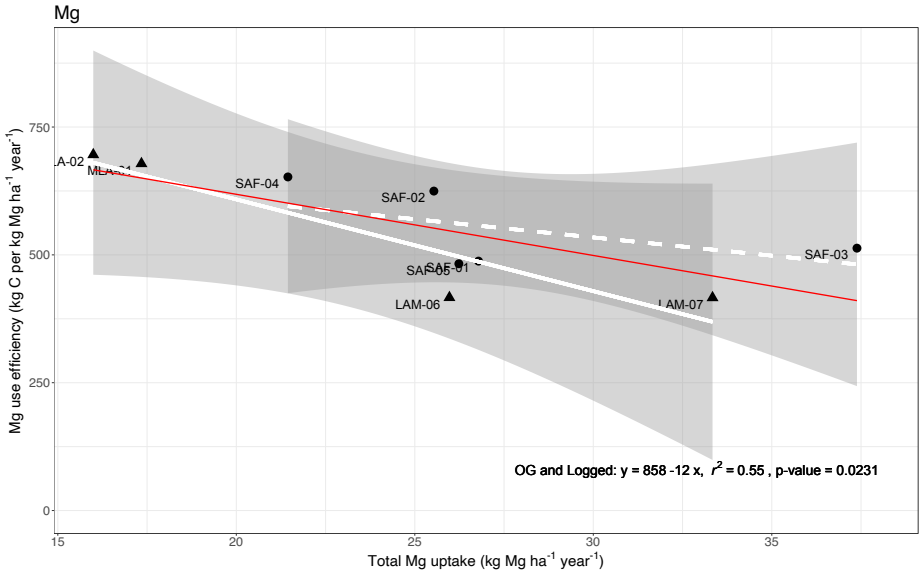


Figure 6.4 Linear relationship, with confidence bands, of total nutrient uptake and nutrient use efficiency.

The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). Significant lines by forest type are shown in black and non-significant lines in white. Regression equation is shown for significant regressions. The red lines for P and Mg are linear regressions fitted across forest types and the red line for Ca is a segmented regression fitted across forest types. The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (circles, MLA-02, MLA-01, LAM-07 and LAM-06) and logged (triangles, SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1.

For N, there was no significant relationship for either forest type, or for both forest types in combination (Fig. 6.4).

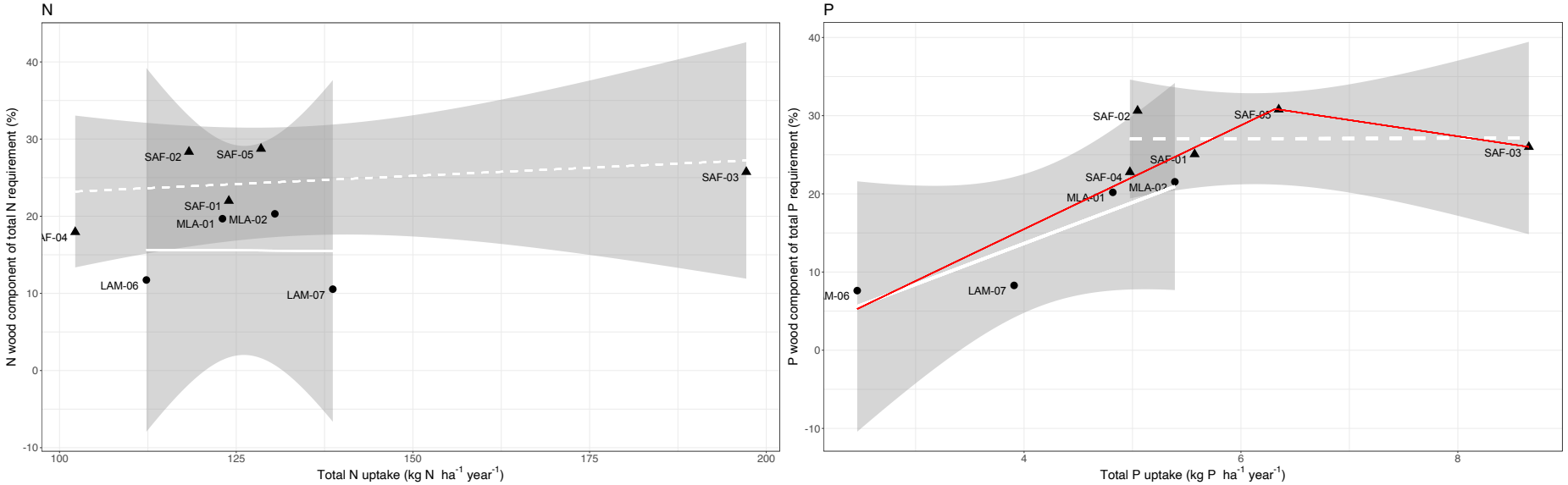
For P, there was a negative relationship for both old-growth and logged forests (Fig. 6.4). The lines intersect and have a similar slope, indicating single overall negative relationship. While the relationship with neither forest type individually was significant, the overall regression combing both forest types was significant, and was an extension of the same relationships found within a forest type.

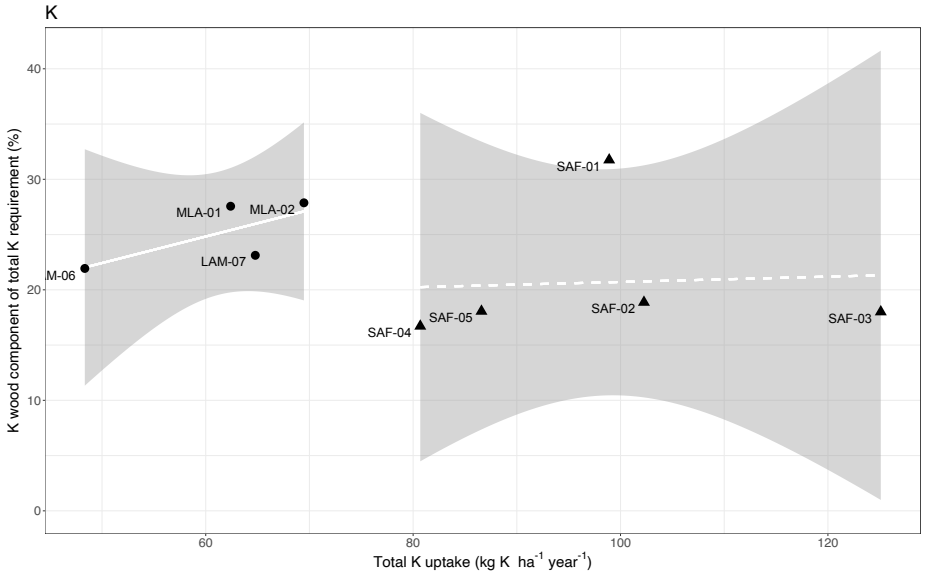
For K, there was no relationship, and strikingly little variance in K use efficiency across a fairly large range of uptake rates or across both forest types (Fig. 6.4).

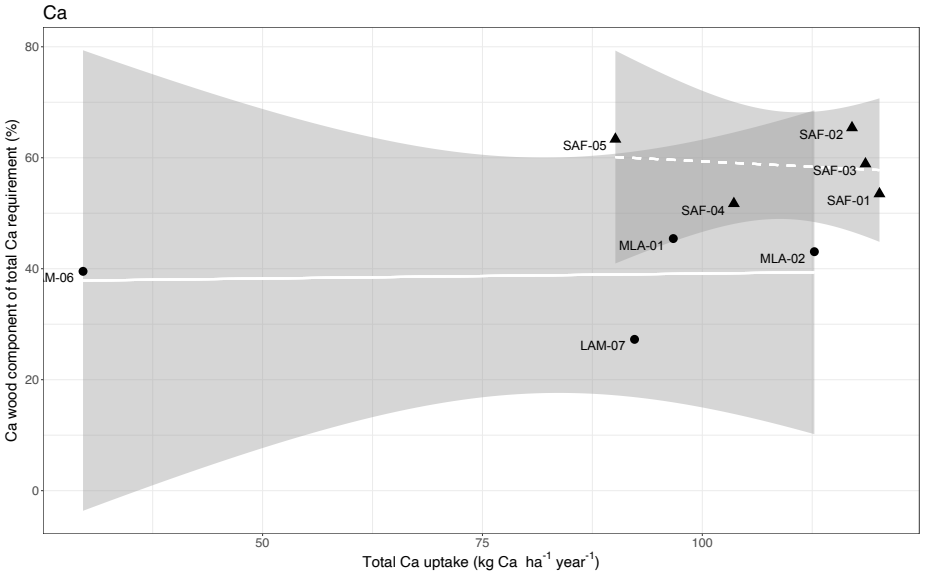
For Ca, there was no relationship in almost all sites, but strong divergence in one Ca-limited site (LAM-06), which drove the strong negative relationship in old-growth forests and a strong threshold relationship overall. Based on the segmented regression ($p=0.007$), the threshold uptake rate was 98.94±7.80 kg Ca/ha/year. It is important to note, however, that due to the uneven distribution of the data along the Ca uptake axis, the threshold point cannot be reliably determined and could be anywhere between ~50-100 kg Ca/ha/year.

For Mg, there was a weak negative and broadly consistent relationship in both old-growth and logged forests. The individual relationship was not significant in either forest type, but the overall regression was significant.

Q5) Can allocation shifts to wood explain how NPP is maintained in nutrient-poor sites?




K
K wood component of total K requirement (%)
Total K uptake (kg K ha-1 year-1)
SAF-01
MLA-01
MLA-02
LAM-07
M-06
SAF-04
SAF-05
SAF-02
SAF-03


Ca
Ca wood component of total Ca requirement (%)
Total Ca uptake (kg Ca ha-1 year-1)
SAF-05
SAF-02
SAF-03
SAF-04
SAF-01
MLA-01
MLA-02
M-06
LAM-07

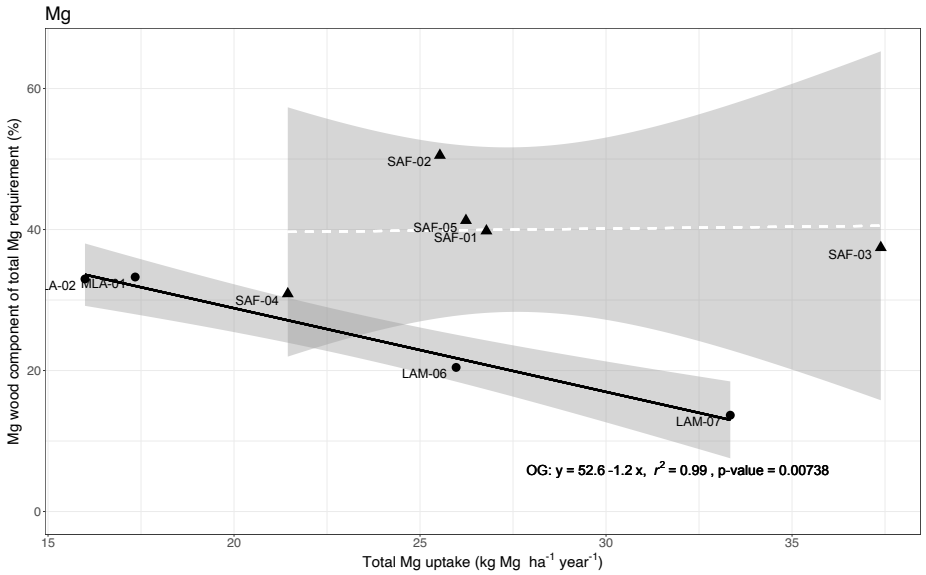

Mg
Mg wood component of total Mg requirement (%)
Total Mg uptake (kg Mg ha-1 year-1)
SAF-02
SAF-05
SAF-01
SAF-03
SAF-04
LAM-06
LAM-07
OG: y = 52.6 -1.2 x, r2 = 0.99 , p-value = 0.00738

Figure 6.5 Linear relationship, with confidence bands, of total nutrient uptake and the woody component of nutrient requirement.

The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). Significant lines by forest type are shown in black and non-significant lines in white. Regression equation is shown for significant regressions. The red line for P is a segmented regression fitted across forest types (marginally significant, p=0.052). The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (circles, MLA-02, MLA-01, LAM-07 and LAM-06) and logged (triangles, SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1.

For N, K and Ca, there was no relationship between nutrient uptake from soil and the allocation of nutrient requirement to the woody component (Fig. 6.5).

For P, there was a positive, but non-significant relationship in old-growth forests. There was also some indication for a threshold uptake at 6.32±0.73 kg P ha/year, but this was only marginally significant ($p=0.052$). However, the positive relationship is contrary to the hypothesis of increased investment in wood under low uptake rates. Logged forests had a higher allocation to wood than old-growth forests, and no relationship with nutrient uptake.

For Mg, there was a negative relationship in old-growth forests, indicating that more Mg is stored in wood in Mg poor sites. There was no relationship in logged forests.

DISCUSSION

No relationship between NPP and soil nutrient content

We found no relationship between NPP and any of the elements. Contrary to our hypothesis, NPP did not increase with soil P content or with any other soil nutrient variable. We can offer five possible explanations for the lack of pattern between NPP and soil nutrients, which are related to our research questions. One possibility is that measured soil nutrient stocks may be a poor metric of how available that particular

nutrient is to plants, depending on which from the nutrient is in. We discuss this possibility later, but this is why we use nutrient uptake rates as the x-axis variable in subsequent analyses, as the variable better reflects what is available or required by plants. The four other explanations shape our research questions. First, *uptake rates do not vary with soil nutrient status*. Nutrient content is adequate for the nutrient requirement of NPP in all of our sites, and therefore nutrient uptake is not constrained by soil nutrient content. Second, *nutrient resorption rates adjust* so that in nutrient poor soils more of the nutrient requirement is met by resorption, thus breaking the link between soil nutrients and NPP. Third, *nutrient use efficiency changes*, so that less nutrients are required per unit of biomass production. Fourth, *allocation shifts*, so that aspects of NPP that require low nutrient concentrations (e.g. wood production) increase at the expense of aspects (canopy leaves) that have high nutrient requirement. We discuss these aspects collectively considering each nutrient in turn.

Nitrogen

Overall our results suggest there is very little evidence that N content is limiting across all sites. We find that there is no relationship between soil N concentration and uptake of N. This suggests that soil N content is adequate for what is needed for NPP. The weak evidence of ecosystem level responses to variation in N content support this – there is very little variation in resorption rates, or in nitrogen stoichiometry. N appears sufficient in all plots and there is little need to invoke trade-offs or strategies to maintain N content. This study provides strong mechanistic evidence of lack of N limitation in both old-growth and logged forests. There might be a small effect in old-growth forests,

with some hint of slightly higher N use efficiency in low N content forests.

Phosphorus

Overall, P shows the opposite story to N. When P cycle variables are plotted against uptake, clear ecosystem properties emerge that are largely consistent across both old-growth and logged forests. Decreased P uptake leads to increased adoption of resorption as a strategy, but there is a non-linear threshold phenomenon that cuts in when P uptake is 5.05±0.20 kg P/ha/year. This suggests a tradeoff at this point, below which it is less costly to invest in resorption than in enhanced P uptake from the soil. The old-growth forests tend to sit at or below this threshold, and logged forests at or above. The relationship is much clearer when P uptake rate is the x-axis rather than soil P concentration. This may reflect the different forms of P in logged vs old-growth forests; there is possibly more P in available forms in logged forests because of soil organic debris from past logging events or because of higher debris input due to the current higher mortality rate (Riutta et al., 2021).

Phosphorus stoichiometry (P use efficiency) also reflects uptake rates: when less P is available the P concentration in tissues reduces. It remains unclear what physiological costs such low P invokes, but this suggests some of the P in tissue may not be metabolically essential (e.g. as storage in leaf vacuoles or as oxalate crystals in hardwood). Increased allocation to wood production at the expense of leaf production is not a relevant factor in buffering NPP against poor soil P content. In fact, there is a hint of an opposite pattern, with low P content sites storing less P in wood.

Our results provide mechanistic insights into previously reported P limitation in tropical forests. Most of the existing evidence is, however, correlational. This study shows clear mechanistic evidence of soil P limitation in old-growth forests, and such limitation induces ecosystem strategies (resorption) to compensate for low content. It seems that the logged forests in general have sufficient available P for shifts in ecosystem resorption not to be invoked, though stoichiometry does adjust to reflect low P content. It also shows why purely correlational analysis (e.g. plotting NPP or woody growth against soil P) are very difficult to interpret.

Potassium

Potassium shows a broadly similar pattern to P, however, these patterns are weaker and therefore inconclusive. The old-growth forests show increased resorption when K content is low, while logged forests seem to have sufficient soil K content. However, unlike for P, there is no variation in K use efficiency with uptake rate. The stoichiometry of K seems relatively invariant: this suggests that all the K in organs is required for essential metabolic purposes, and there is little flexibility in shifting K concentrations or downregulating K metabolism.

Calcium

Overall, Ca content seems sufficient in all sites except one, LAM-06, which has exceptionally low soil Ca. When LAM-06 is excluded, there is no relationship between soil Ca, Ca uptake or Ca use efficiency, indicating Ca content is sufficient in all these

other cases both in old-growth and logged forests. In LAM-06, we do see clear evidence of Ca content being an issue: Ca uptake rates drop substantially, and Ca stoichiometry shifts substantially to less than half the concentrations of other sites. As Ca cannot be resorbed, shifting stoichiometry is the only strategy available under limited soil Ca. The maintenance of fairly high NPP at LAM-06 suggests that low Ca is not a major constraint on productivity, but it may invoke some metabolic costs. The substantially different species composition at LAM-06 compared to the adjacent LAM-07 may be partially driven by adaptation to low Ca content (as well as low P content and different soil moisture retention).

Magnesium

As expected, Mg broadly shows no relationship to soil Mg content, indicating it is broadly available in sufficient quantities. Mg is the one element that shows more investment in woody storage when Mg content is low. It is interesting to speculate if there is a mechanism underlying this. However, as it is very unlikely that Mg limits productivity in these sites, it is unlikely that this explains the invariance of NPP with soil nutrient status.

CONCLUSIONS

Overall, our study shows interesting contrasts in how ecosystem nutrient cycles adjust to limitations on uptake rate. At one extreme, N seems to be in ample supply at all

sites and there is no evidence of adjustments in ecosystem strategy (resorption or stoichiometry) induced by limited N supply. Mg shows a broadly similar pattern to N, though with some non-significant suggestions of shifts in stoichiometry and resorption. If there are threshold uptake rates for these two nutrients, they are below the ranges observed in our plots.

The remaining three nutrients (P, K, and Ca) show evidence of threshold behavior in our plots, indicating that at least some plots are limited in supply of these nutrients and showing ecosystem-level response strategies. Interestingly, there are contrasting responses in each of the three nutrients. For Ca, resorption is not an option and so shifting stoichiometry is the only option to maintain NPP. Limited Ca supply seems to be an issue at only one of our sites, the sandy LAM-06 site, and may partially account for the high species turnover between this plot and the adjacent LAM-05 plot. For K, in strong contrast, we see striking evidence that shifting stoichiometry is not a feasible option (or is a costly option), and the limited K supply in the old-growth plots seems to be compensated for by higher K resorption rates. Phosphorus, on the other hand, adopts a combined strategy, shifting both resorption rates and stoichiometry when uptake rates become restricted. Hence some of the P in biomass may not be metabolically essential, allowing some flexibility in P stoichiometry, whereas the rest of the P and all of the K does appear metabolically essential. We note that in comparing across plots we are incorporating shifts in community composition in our analysis. Shifts in nutrient strategy may reflect in species composition, with species better adapted to exploit low supply of rock-weathered nutrients predominating in

some sites. In addition, there is the possibility of shifts in mycorrhizal community composition across soil environments (Peay et al., 2010, Peay et al., 2015).

Overall, this study demonstrates that a whole forest nutrient approach can reveal new insights. We have shown how limited supply of P, K and Ca is a challenge in lowland tropical forest ecosystems, and how different strategies are adopted to compensate for low supply of each nutrient. These insights also explain why it is challenging to determine a simple relationship between NPP and soil nutrient content in wet tropical rainforests: a number of compensation strategies, different for each limiting nutrient, diffuse the relationship between nutrient supply and ecosystem productivity.

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Sabah Biodiversity Centre, Maliau Basin Management Committee, and Forest Department Sarawak for permitting research in the SAFE Project (Access Licence: JKM/MBS.1000-2/2 (187)), Maliau Basin Conservation Area, and Lambir Hills National Park (Permit no. NCCD.907.4.4(JLD.10)-117 and park permit no. 66/2014) respectively.

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SUPPORTING INFORMATION

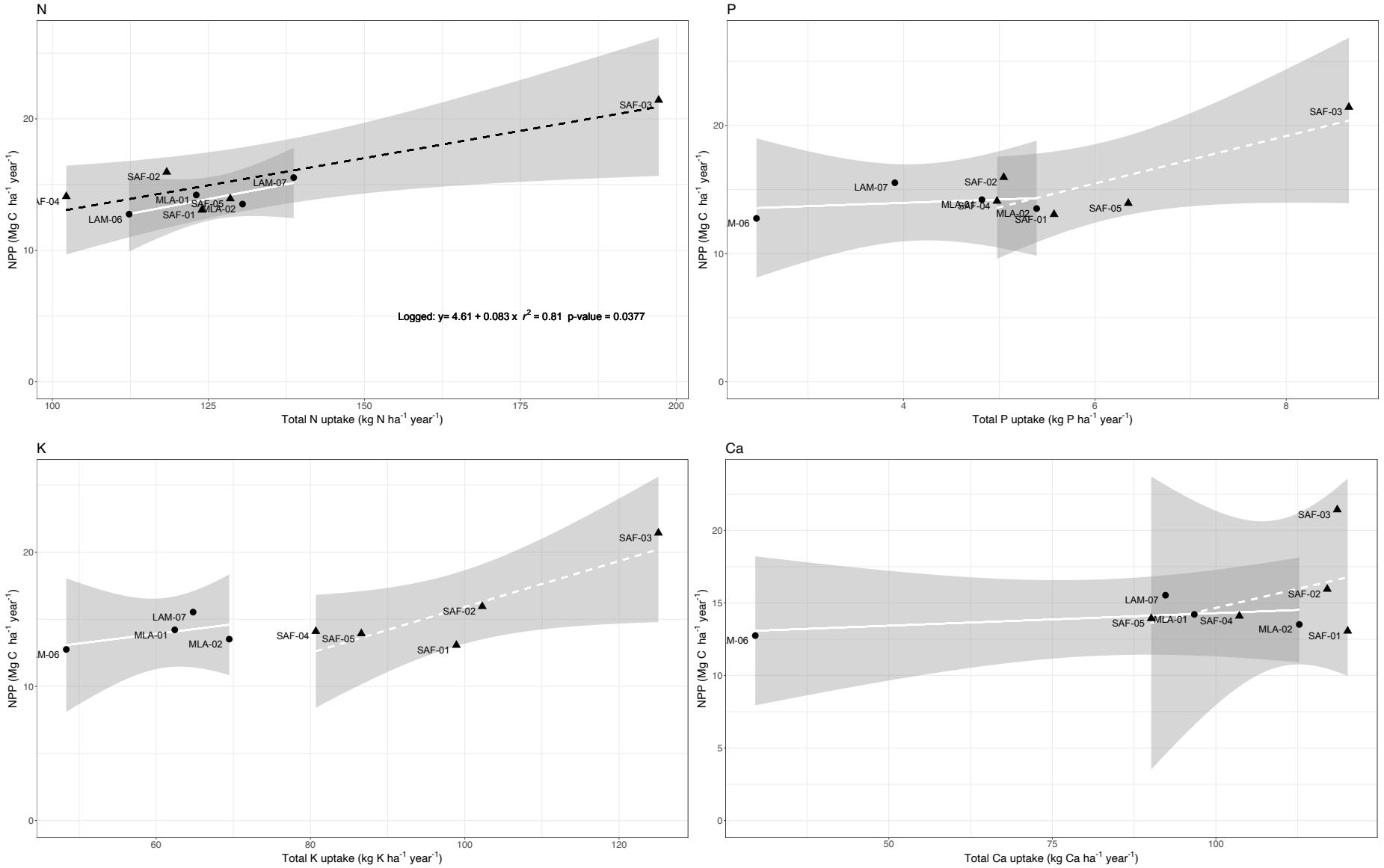
Table S6.1. Soil characteristics of the study plots. Weighted mean concentrations of total C, N, P, K Ca, Mg, effective cation exchange capacity (eCEC), pH (H_2O), sand and clay ratio by subsoil layer depth from 30 cm up to 300 cm.

Plot code	C (%)	N (%)	P (mg/kg)	K (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	eCEC (mmol+/kg)	pH	Sand (%)	Silt (%)	Clay (%)
SAF-01	0.30	0.049	270.09	99.00	27.39	43.18	53.88	4.95	52.45	36.82	10.74
SAF-02	0.16	0.038	331.09	115.17	366.84	291.43	70.84	5.44	40.24	45.90	13.85
SAF-05	3.97	0.317	408.99	45.79	245.20	468.07	57.21	5.74	13.37	56.75	29.87
SAF-04	0.56	0.116	122.36	34.84	13.54	30.31	42.22	4.47	59.84	34.98	5.19
SAF-03	0.41	0.105	75.05	49.48	16.48	11.68	27.49	4.74	67.56	22.33	10.10
MLA-02	1.35	0.181	163.82	55.70	4.86	9.30	50.93	4.89	43.62	37.37	19.02
MLA-01	0.29	0.069	118.34	80.07	6.15	41.69	55.17	5.03	43.46	37.44	19.10
LAM-07	0.29	0.047	NA	18.98	2.43	6.78	37.85	3.79	42.40	31.79	25.81
LAM-06	0.09	0.020	NA	24.62	1.44	1.88	16.53	4.81	68.68	16.06	15.26

Table S6.2. Proportion of sampled basal area (BA)

Plot code	BA total m^2 ha^{-1}	BA of sampled families	BA of sampled genera	BA of sampled species	Sampled family proportion	Sampled genus proportion	Sampled species proportion
SAF-01	7.31	4.68	3.40	2.07	0.64	0.46	0.28
SAF-02	12.20	7.44	7.15	5.85	0.61	0.59	0.48
SAF-05	13.89	8.52	5.81	4.34	0.61	0.42	0.31
SAF-04	19.65	4.73	2.64	0.21	0.24	0.13	0.01
SAF-03	23.35	13.33	10.88	5.09	0.57	0.47	0.22
MLA-	34.72	25.64	9.36	3.82	0.74	0.27	0.11

02							
MLA-01	41.30	32.15	19.71	9.19	0.78	0.48	0.22
LAM-07	31.84	13.83	12.49	5.99	0.43	0.39	0.19
LAM-06	41.07	27.13	13.87	5.17	0.66	0.34	0.13


N
NPP (Mg C ha-1 year-1)
Total N uptake (kg N ha-1 year-1)
Logged: y= 4.61 + 0.083 x r2 = 0.81 p-value = 0.0377
SAF-03
SAF-02
LAM-07
MLA-01
SAF-05
MLA-02
SAF-01
LAM-06
P
Total P uptake (kg P ha-1 year-1)
K
Total K uptake (kg K ha-1 year-1)
SAF-04
Ca
Total Ca uptake (kg Ca ha-1 year-1)

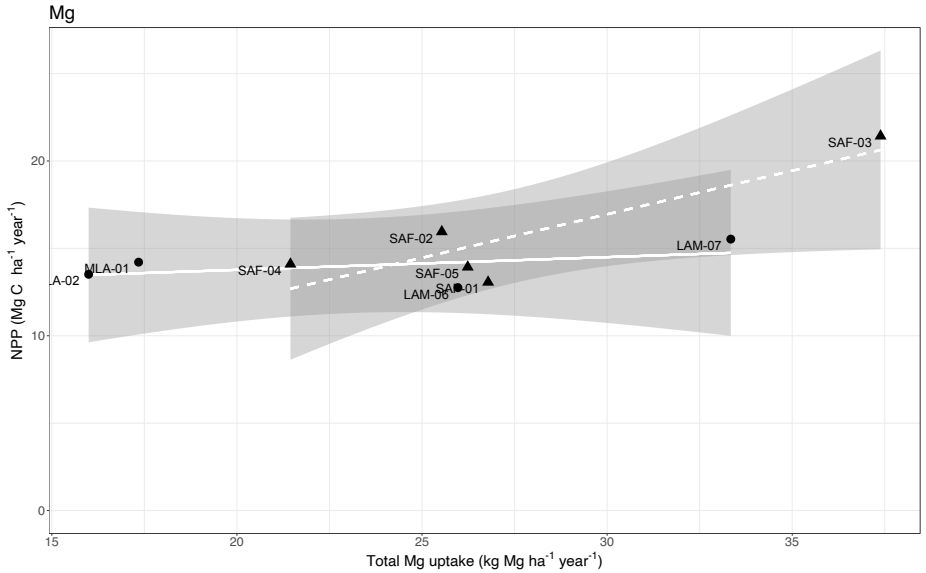


Figure S6.1. Linear relationship, with confidence bands, of total nutrient uptake and net primary productivity (NPP). The model was fitted separately for old-growth forest (continuous line) and logged forest (dashed line). Significant lines are shown black and non-significant lines in white. Regression equation is shown for significant regressions. The values were averaged within each plot. Each data point is one forest plot, grouped into old-growth (MLA-02, MLA-01, LAM-07 and LAM-06) and logged (SAF-01, -02, -03, -04, and -05) forests. For plot descriptions, see Table 6.1.

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Chapter 7 DISCUSSION

This chapter summarises key research findings from my research. It then identifies broader implications and future research.

7.1 Key research findings

Chapter 4

This research has contributed towards addressing several knowledge gaps in the nutrient dynamics of tropical forests. Chapter 4 reports one of the largest datasets of wood nutrient concentrations, and is, to my best knowledge, the first one to examine the radial and vertical nutrient concentration variation in tropical trees. Furthermore, it provides the first estimates for five macronutrients in coarse roots of tropical trees. I observed wood resorption in dipterocarp species, which suggests an efficient nutrient conservation mechanism specific to this particular family. The lower wood nutrient concentrations in dipterocarps compared to other species are largely compensated for by wood resorption during sapwood senescence.

Chapters 5 and 6

Chapters 5 and 6 are based on a novel approach of combining estimates of net primary productivity (NPP) with leaf, wood and fine root stoichiometry to provide direct estimates of fluxes and allocation of nutrients within forest ecosystems. This method was developed and pioneered in this DPhil project. It has since been replicated in Global Ecosystem Monitoring plots in Brazil (M. Scalon et al., unpublished manuscript)

and data collection is underway or planned for other tropical and temperate sites. Chapter 5 provides the first detailed estimates of the nutrient dynamics and shows how logging disturbance affects them. The largest differences were the allocation patterns, with higher amount of nutrients allocated to wood at the expense of canopy, and the lower contribution of leaf resorption towards meeting the nutrient requirement in logged forests compared with old-growth forests. While nutrient use efficiencies showed large variation across plots, this variation was not related to logging disturbance.

In Chapter 6, I examined the relationship between soil nutrients, NPP and nutrient dynamics, which revealed substantial variation in nutrient uptake and allocation across plots. NPP did not correlate with soil nutrient availability of any elements, suggesting soil availability is a weak predictor of NPP in this study. Depending on the nutrient, different strategies, namely changes in resorption rates, changes in nutrient uptake efficiency or nutrient use efficiency, or changes in allocation from nutrient demanding foliar tissue to less demanding woody tissue, are adopted to compensate for low supply of that nutrient. This also explains why it is challenging to determine a simple relationship between NPP and soil nutrient content in wet tropical rainforests: a number of compensation strategies, diffuse the relationship between nutrient supply and ecosystem productivity. This coupling of NPP and stoichiometry shows much potential in advancing the field of ecosystem science.

Below, I synthesise the results by each nutrient, with diagrams of nutrient stocks and fluxes in the old-growth and logged forest ecosystems (Fig. 7.1) and wood nutrient

concentrations within an individual dipterocarp and pioneer tree (Fig. 7.2, 7.3 and 7.4).

Nitrogen

Nitrogen stock in the soil is much larger than the N stock in vegetation, with twice as much N in the top 30 cm of soil as in vegetation. This study provides multiples lines of strong mechanistic evidence of lack of N limitation in both old-growth and logged forests. There appears to be plentiful available N in the soil, hence N appears sufficient in all plots and there is little need to invoke trade-offs or strategies to maintain N content. Some literature from Amazonia suggests that N can be limiting in secondary forests (Davidson et al., 2004). There we might have expected N limitation in heavily logged forests, but I find no evidence for that. Recovering from logging differs from secondary forest growth in that this is plentifully organic debris in the soil at the start of forest regrowth, and this suggests there is plenty of available N.

Leaf resorption rate of N across sites was 46.9±2.4%, while the wood resorption rate (only dipterocarps) was 25.3±7.1%. A global meta-analysis, which did not include any data from Borneo, reported a very similar leaf resorption estimate of 49.5% (Vergutz et al., 2012).

Phosphorus

There was evidence of P limitation in the old growth forests but not in the logged forests. Under limiting P conditions, there was a combined strategy of both increased resorption rates and increased nutrient use efficiency. As an example, there was an exceptionally large discrepancy on the contribution of P resorption to P requirement between LAM-06 site on a P poor sandy soil (resorption contribution of 62.3%) and MLA-01 site on a moderately P rich soil (resorption contribution of 35.6%). Furthermore, the P poor Lambir sites (LAM-6 and LAM-07) showed considerably high P use efficiency. Compared to the other elements, the use efficiency of P was particularly high, 10-20 higher than N, K and Ca use efficiency. I identified a threshold P uptake rate of 5 kg P ha^{-1} $year^{-1}$, below which limitation strategies such as increased leaf resorption were employed. The logged forests appeared to sit at or above this threshold, probably because of substantial organic debris on and in the soil. There is nine times has much P in the soil as in vegetation, but it is quite possible that much of this is in occluded and unavailable forms.

Leaf resorption rate of P across sites 62.1±3.6% while the wood resorption rate (only dipterocarps) was 62.7±11.9%. The global meta-analysis reported a very similar leaf resorption estimate of 59.3% (Vergutz et al., 2012).

Potassium

For K, vegetation stocks exceed the soil stock by 2-5 times (unlike for N and P). Old-growth forests show increased resorption when K content is low, while logged forests

seem to have sufficient soil K content. However, unlike for P, there is no variation in K use efficiency with uptake rate. The stoichiometry of K seems relatively invariant: this suggests that all the K in organs is required for essential metabolic purposes, and there is little flexibility in shifting K concentrations or downregulating K metabolism. Along the logging disturbance gradient, there was lower K resorption and higher uptake towards more disturbed sites.

Leaf resorption rate of K across sites 57.8±3.2% while the wood resorption rate (only dipterocarps) was 56.2±12.5%. A global meta-analysis, which did not include any data from Borneo, reported a very similar leaf resorption estimate of 51.9% (Vergutz et al., 2012).

Calcium

Calcium stock in vegetation is almost ten times larger than Ca stock in soil in old-growth forests, but only of roughly similar magnitide to soil stock in logged forests. Most of the Ca stock in an old-growth forest is the heartwood. However, there was no evidence for Ca limitation, except for one particularly Ca poor site, LAM-06. In that site, Ca uptake rates drop substantially, and Ca stoichiometry shifts substantially to less than half the concentrations of other sites. As Ca cannot be resorbed from senenscent leaves, shifting stoichiometry is the only strategy available under limited soil Ca.

The concentration of Ca in bark was particularly high compared to the concentration

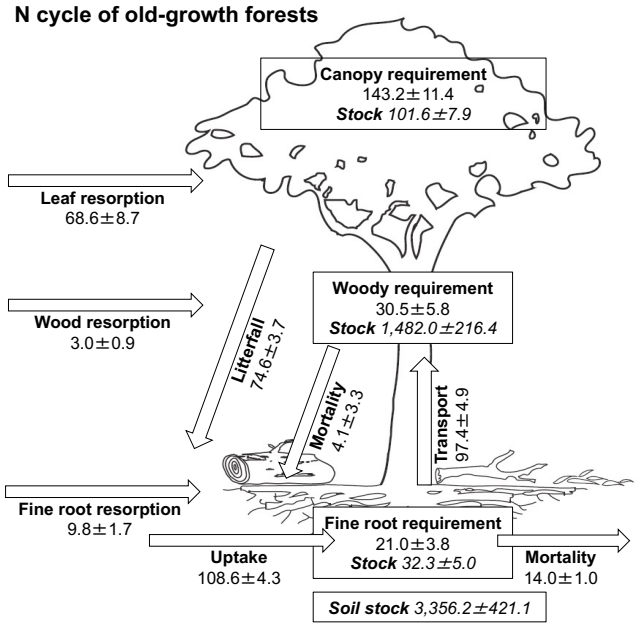
in wood.

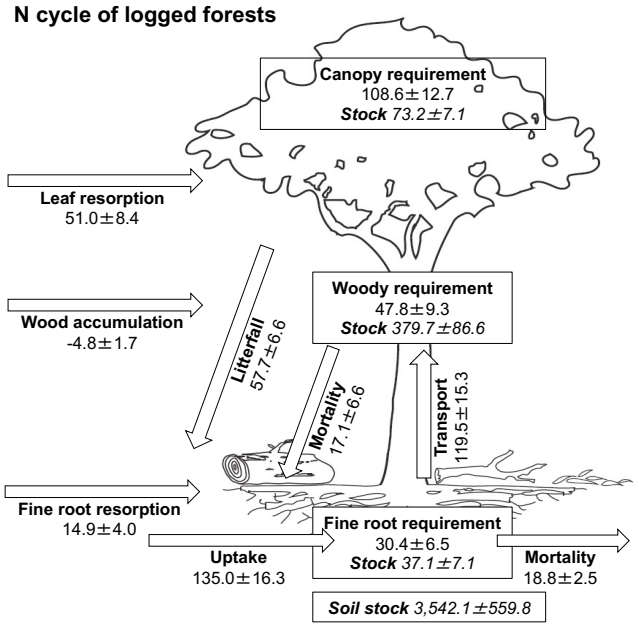
As Ca is an immobile element, there was no leaf resorption of Ca. Ca was also found to increase in heartwood compared to sapwood, most likely in the form of oxalate crystals. It is possible that this concentration of Ca in the heartwood has a functional role in strengthening tree structure. It is interesting to speculate if the Ca stored in heartwood is entirely unavailable, or potentially acts as a store that buffers low Ca availability from the soil. In temperate forests, re-translocation of Ca from heartwood to sapwood has been observed (Andrews et al., 1999).

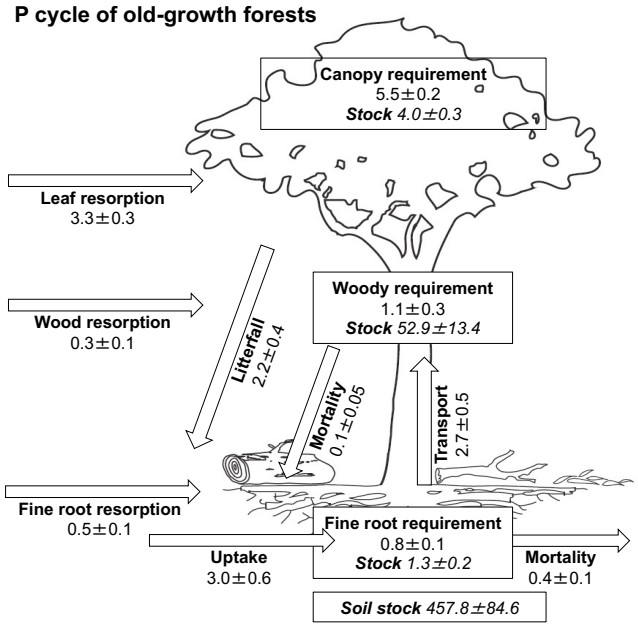
Magnesium

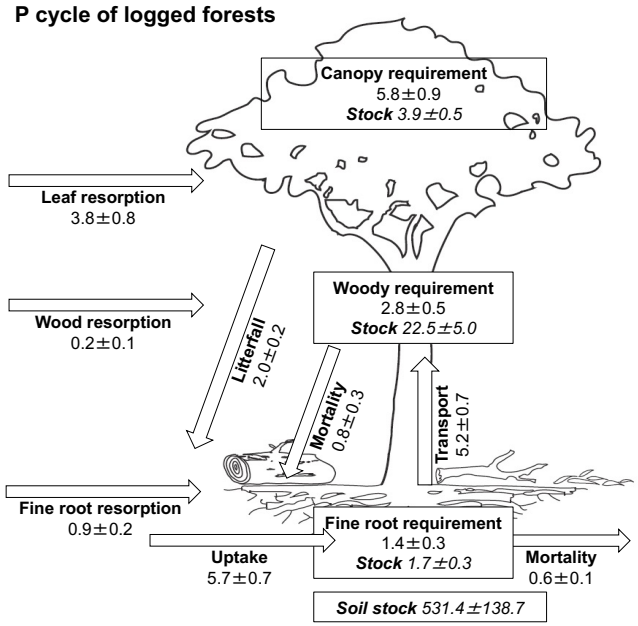
Magnesium stock in vegetation is twice as high than Mg stock in soil in old growth forests, but only a third as high in logged forests. There was no evidence in Mg limitation, indicating it is broadly available in sufficient quantities. Mg was the only element that showed more investment in woody storage when Mg content is low. Magnesium use efficiency was larger than that of N, K and Ca, but not as high as that of P. The contribution of leaf resorption to the total Mg requirement was very small in logged forests, but substantial in old-growth forests.

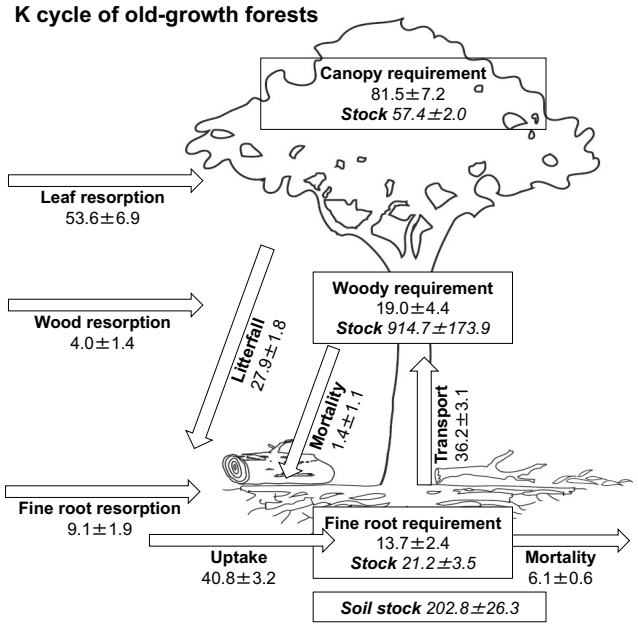
There was very little leaf resorption (16.2±4.2%) and no wood resorption for Mg. The results of the low leaf resorption rate is consistent with a global meta-analysis (14.5%) (Vergutz et al., 2012). As with Ca, the concentration of Mg increases in the heartwood relative to sapwood.

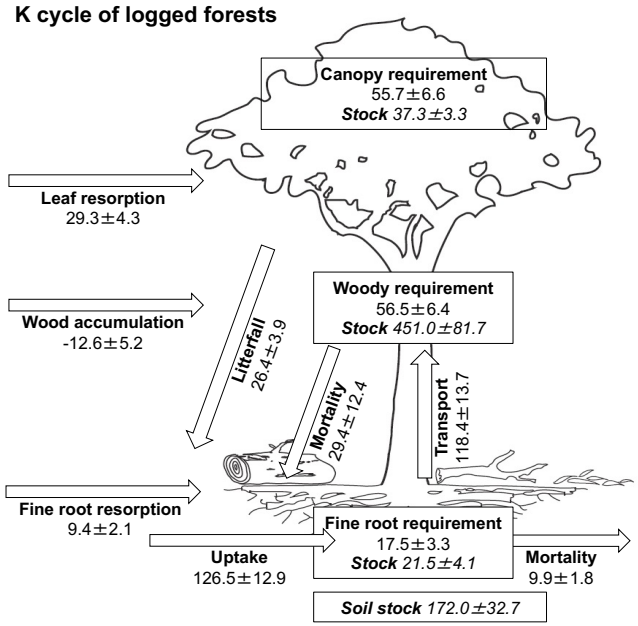

N cycle of old-growth forests
Canopy requirement
143.2±11.4
Stock 101.6±7.9
Leaf resorption
68.6±8.7
Wood resorption
3.0±0.9
Litterfall
74.6±3.7
Woody requirement
30.5±5.8
Stock 1,482.0±216.4
Mortality
4.1±3.3
Transport
97.4±4.9
Fine root resorption
9.8±1.7
Uptake
108.6±4.3
Fine root requirement
21.0±3.8
Stock 32.3±5.0
Mortality
14.0±1.0
Soil stock 3,356.2±421.1

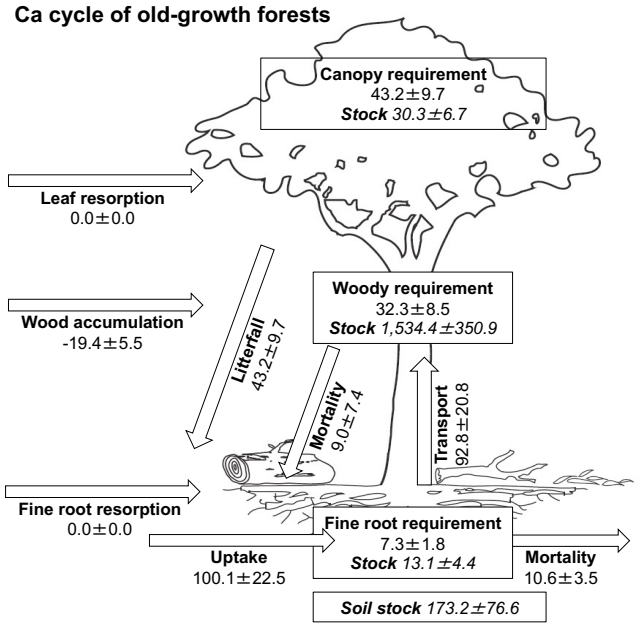

N cycle of logged forests
Canopy requirement
108.6±12.7
Stock 73.2±7.1
Leaf resorption
51.0±8.4
Wood accumulation
-4.8±1.7
Litterfall
57.7±6.6
Woody requirement
47.8±9.3
Stock 379.7±86.6
Mortality
17.1±6.6
Transport
119.5±15.3
Fine root resorption
14.9±4.0
Uptake
135.0±16.3
Fine root requirement
30.4±6.5
Stock 37.1±7.1
Mortality
18.8±2.5
Soil stock 3,542.1±559.8

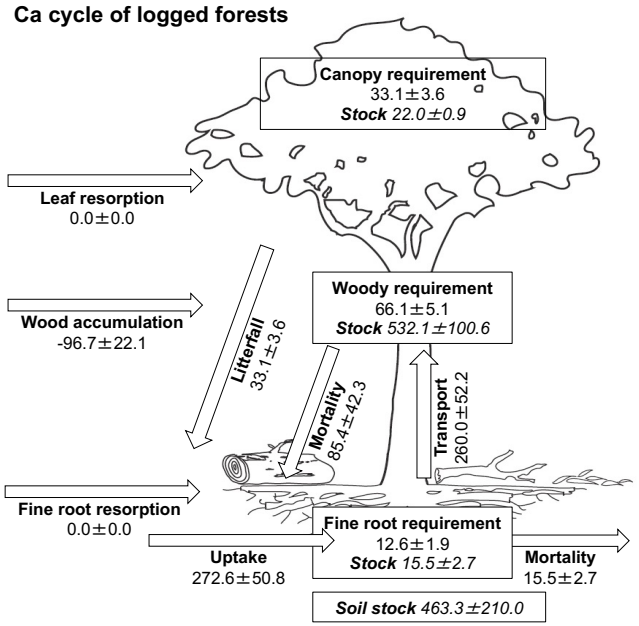

P cycle of old-growth forests
Canopy requirement
5.5±0.2
Stock 4.0±0.3
Leaf resorption
3.3±0.3
Wood resorption
0.3±0.1
Litterfall
2.2±0.4
Woody requirement
1.1±0.3
Stock 52.9±13.4
Mortality
0.1±0.05
Transport
2.7±0.5
Fine root resorption
0.5±0.1
Uptake
3.0±0.6
Fine root requirement
0.8±0.1
Stock 1.3±0.2
Mortality
0.4±0.1
Soil stock 457.8±84.6


P cycle of logged forests
Canopy requirement
5.8±0.9
Stock 3.9±0.5
Leaf resorption
3.8±0.8
Wood resorption
0.2±0.1
Litterfall
2.0±0.2
Woody requirement
2.8±0.5
Stock 22.5±5.0
Mortality
0.8±0.3
Transport
5.2±0.7
Fine root resorption
0.9±0.2
Uptake
5.7±0.7
Fine root requirement
1.4±0.3
Stock 1.7±0.3
Mortality
0.6±0.1
Soil stock 531.4±138.7


K cycle of old-growth forests
Canopy requirement
81.5±7.2
Stock 57.4±2.0
Leaf resorption
53.6±6.9
Wood resorption
4.0±1.4
Litterfall
27.9±1.8
Woody requirement
19.0±4.4
Stock 914.7±173.9
Mortality
1.4±1.1
Transport
36.2±3.1
Fine root resorption
9.1±1.9
Uptake
40.8±3.2
Fine root requirement
13.7±2.4
Stock 21.2±3.5
Mortality
6.1±0.6
Soil stock 202.8±26.3


K cycle of logged forests
Canopy requirement
55.7±6.6
Stock 37.3±3.3
Leaf resorption
29.3±4.3
Wood accumulation
-12.6±5.2
Litterfall
26.4±3.9
Woody requirement
56.5±6.4
Stock 451.0±81.7
Mortality
29.4±12.4
Transport
118.4±13.7
Fine root resorption
9.4±2.1
Uptake
126.5±12.9
Fine root requirement
17.5±3.3
Stock 21.5±4.1
Mortality
9.9±1.8
Soil stock 172.0±32.7


Ca cycle of old-growth forests
Canopy requirement
43.2±9.7
Stock 30.3±6.7
Leaf resorption
0.0±0.0
Wood accumulation
-19.4±5.5
Litterfall
43.2±9.7
Woody requirement
32.3±8.5
Stock 1,534.4±350.9
Mortality
9.0±7.4
Transport
92.8±20.8
Fine root resorption
0.0±0.0
Uptake
100.1±22.5
Fine root requirement
7.3±1.8
Stock 13.1±4.4
Mortality
10.6±3.5
Soil stock 173.2±76.6


Ca cycle of logged forests
Canopy requirement
33.1±3.6
Stock 22.0±0.9
Leaf resorption
0.0±0.0
Wood accumulation
-96.7±22.1
Litterfall
33.1±3.6
Woody requirement
66.1±5.1
Stock 532.1±100.6
Mortality
85.4±42.3
Transport
260.0±52.2
Fine root resorption
0.0±0.0
Uptake
272.6±50.8
Fine root requirement
12.6±1.9
Stock 15.5±2.7
Mortality
15.5±2.7
Soil stock 463.3±210.0

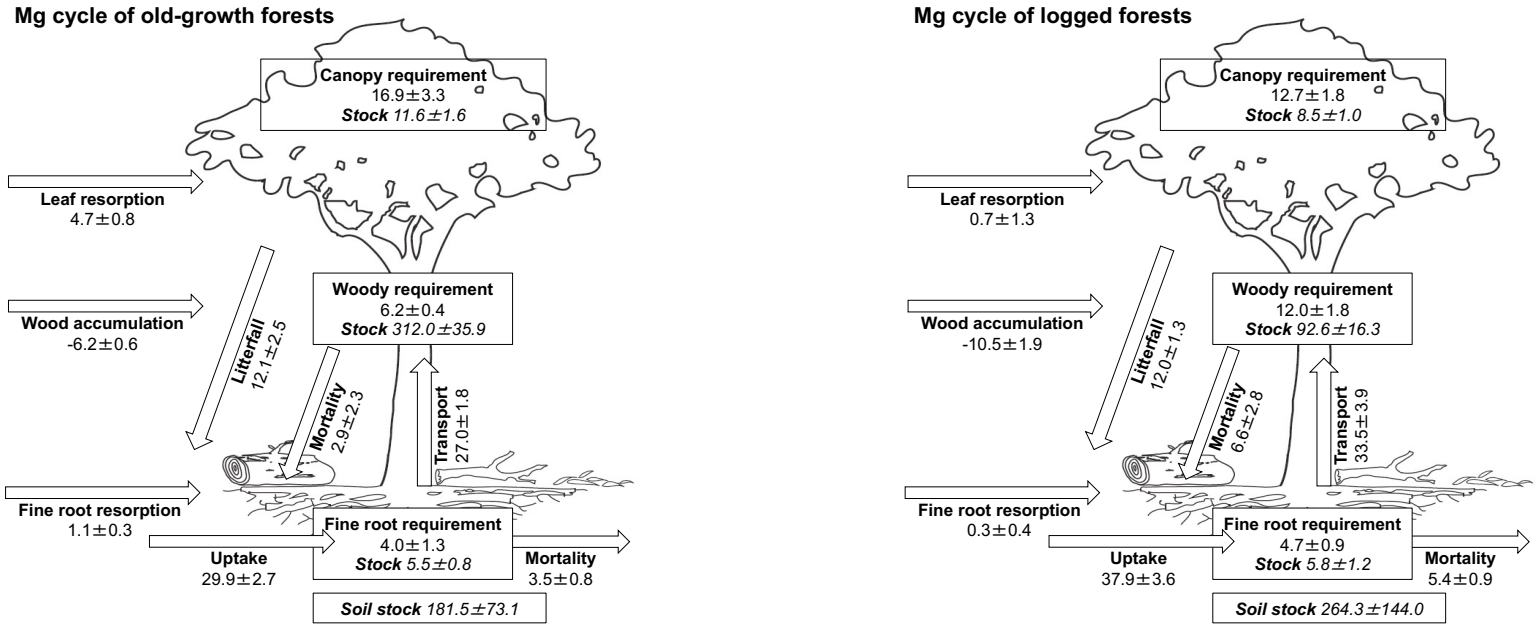


Figure 7.1 Comparison of nutrient cycles between old-growth forests and logged forests

Fluxes are expressed in kg N/P/K/Ca/Mg ha^{-1} $year^{-1}$ and stocks in in kg N/P/K/Ca/Mg ha^{-1}. Soil stock is between 0-30 cm depth. The values were averaged within each plot, and then averaged in each group of old-growth (OG: MLA-02, MLA-01, LAM-07 and LAM-06), and logged (SAF-01, -02, -03, -04, and -05) forests. For plot information, see Chapter 3. Each stock was calculated using C stock (Riutta et al., 2018) and nutrient stoichiometry. Litterfall was calculated as a difference between canopy requirement and leaf resorption. Wood resorption estimates by species groups (dipterocarps, non-pioneers and pioneers) were weighted by the basal area proportion of each group within each plot. Nutrient transport is a difference between total aboveground requirement

and resorption. Root mortality was calculated by assuming the fine root residence time was equal to fine root stock divided by fine root productivity. Fine root resorption was set to be equal to leaf resorption due to data unavailability. Nutrient uptake is a difference between total requirement and leaf resorption.

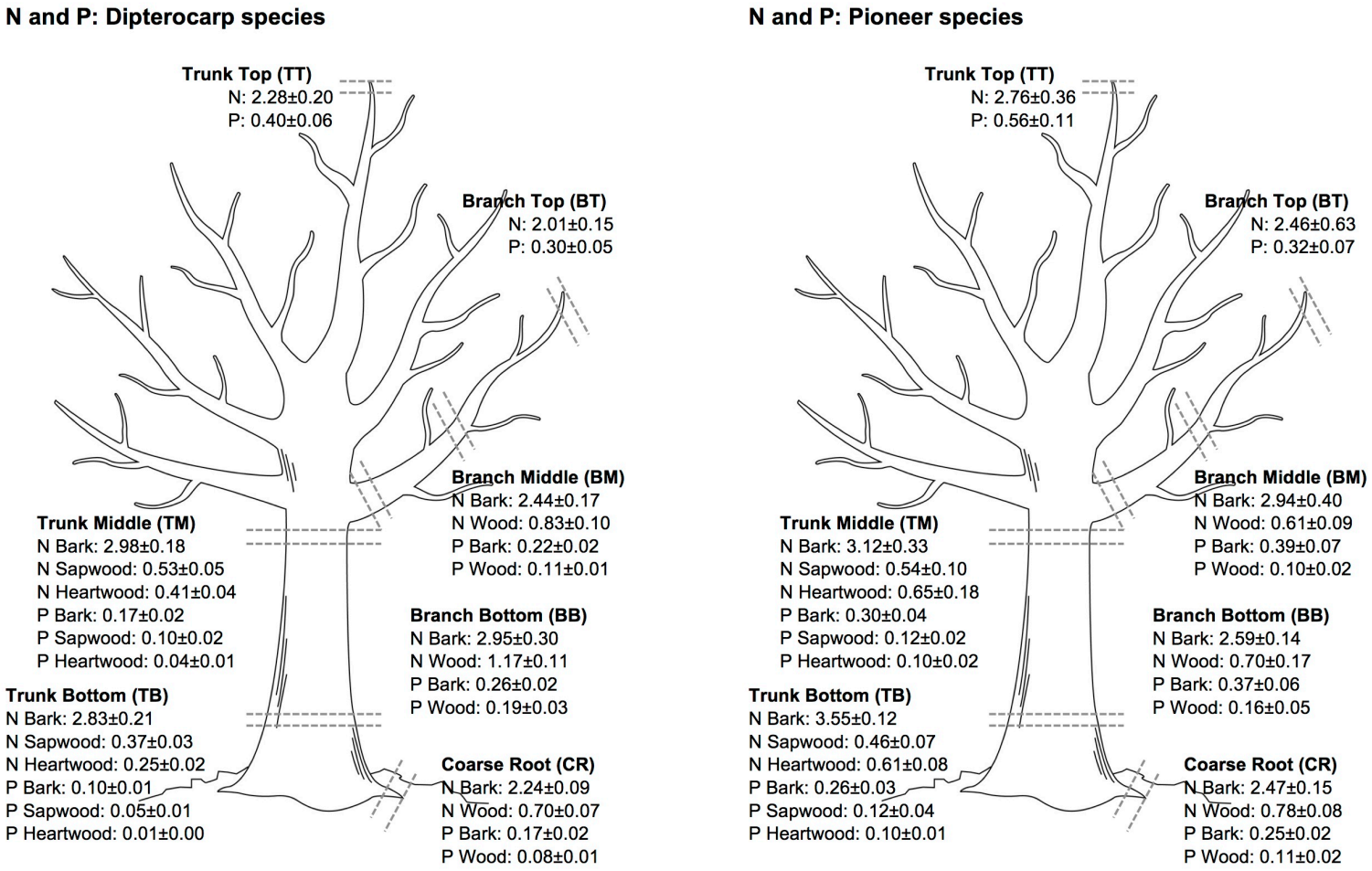


Figure 7.2 Variation of wood N and P concentrations within a whole tree of Dipterocarp and pioneer species

Values (±SE) are in mg/g, and averaged within five Dipterocarp species: *Parashorea malaanonan*, *Shorea johorensis*, *Shorea leprosula*, *Shorea micans* and

Shorea parvifolia (*n* = 15), and within three pioneer species: *Trema orientalis*, *Macaranga pearsonii* and *Neolamarckia cadamba* (*n* = 9). Trunk samples were partitioned to three sections: bark, sapwood and heartwood. Due to the absence of colour boundary between sapwood and heartwood in most branch and coarse root samples, they were disaggregated into wood and bark only. The tip of sampled trunk and branch was twig-like (less than 2 cm diameter), which was not debarked. See Chapter 4 for further information.

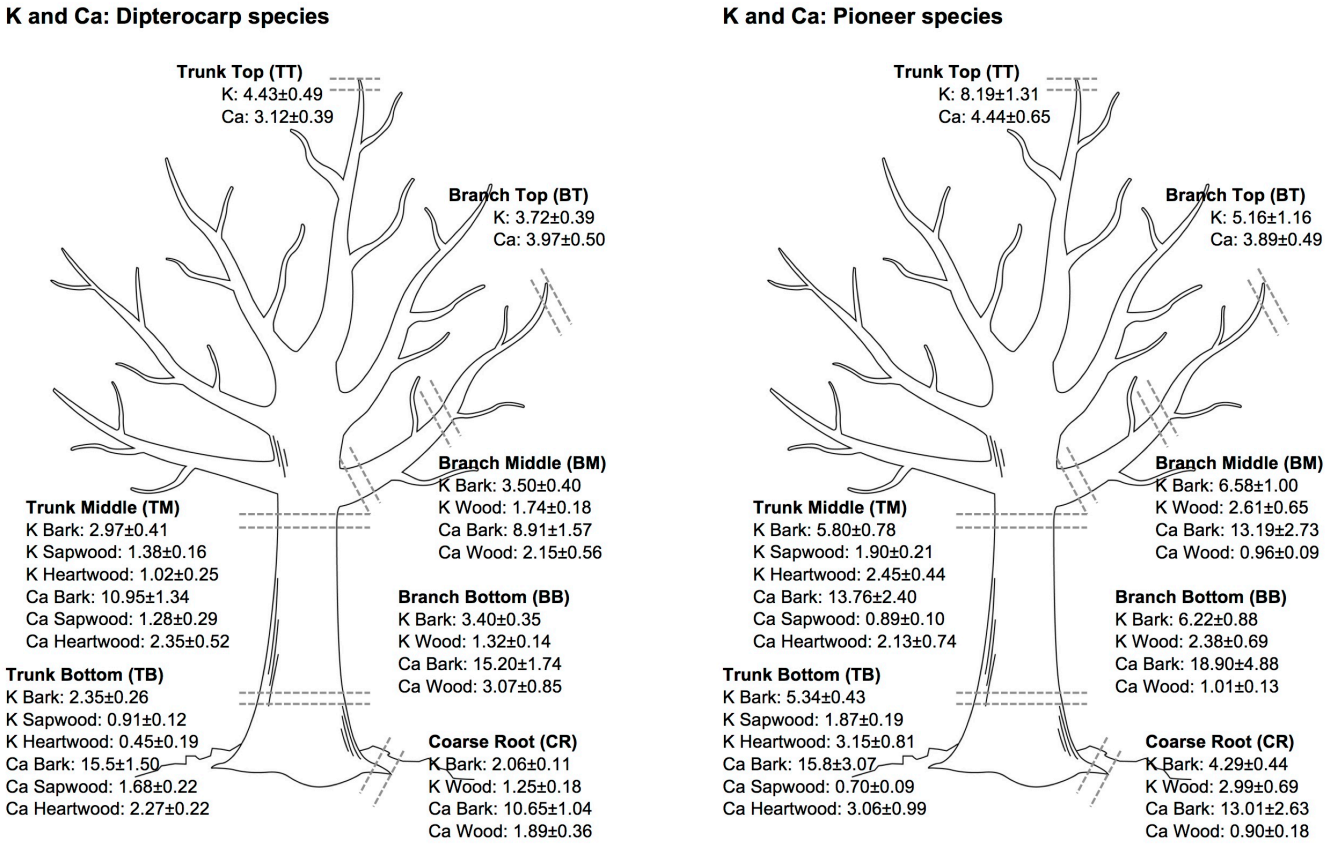


Figure 7.3 Variation of wood K and Ca concentrations within a whole tree of Dipterocarp and pioneer species

Values (±SE) are in mg/g, and averaged within five Dipterocarp species: *Parashorea malaanonan*, *Shorea johorensis*, *Shorea leprosula*, *Shorea micans* and *Shorea parvifolia* (*n* = 15), and within three pioneer species: *Trema orientalis*, *Macaranga pearsonii* and *Neolamarckia cadamba* (*n* = 9). Trunk samples were

partitioned to three sections: bark, sapwood and heartwood. Due to the absence of colour boundary between sapwood and heartwood in most branch and coarse root samples, they were disaggregated into wood and bark only. The tip of sampled trunk and branch was twig-like (less than 2 cm diameter), which was not debarked. See Chapter 4 for further information.

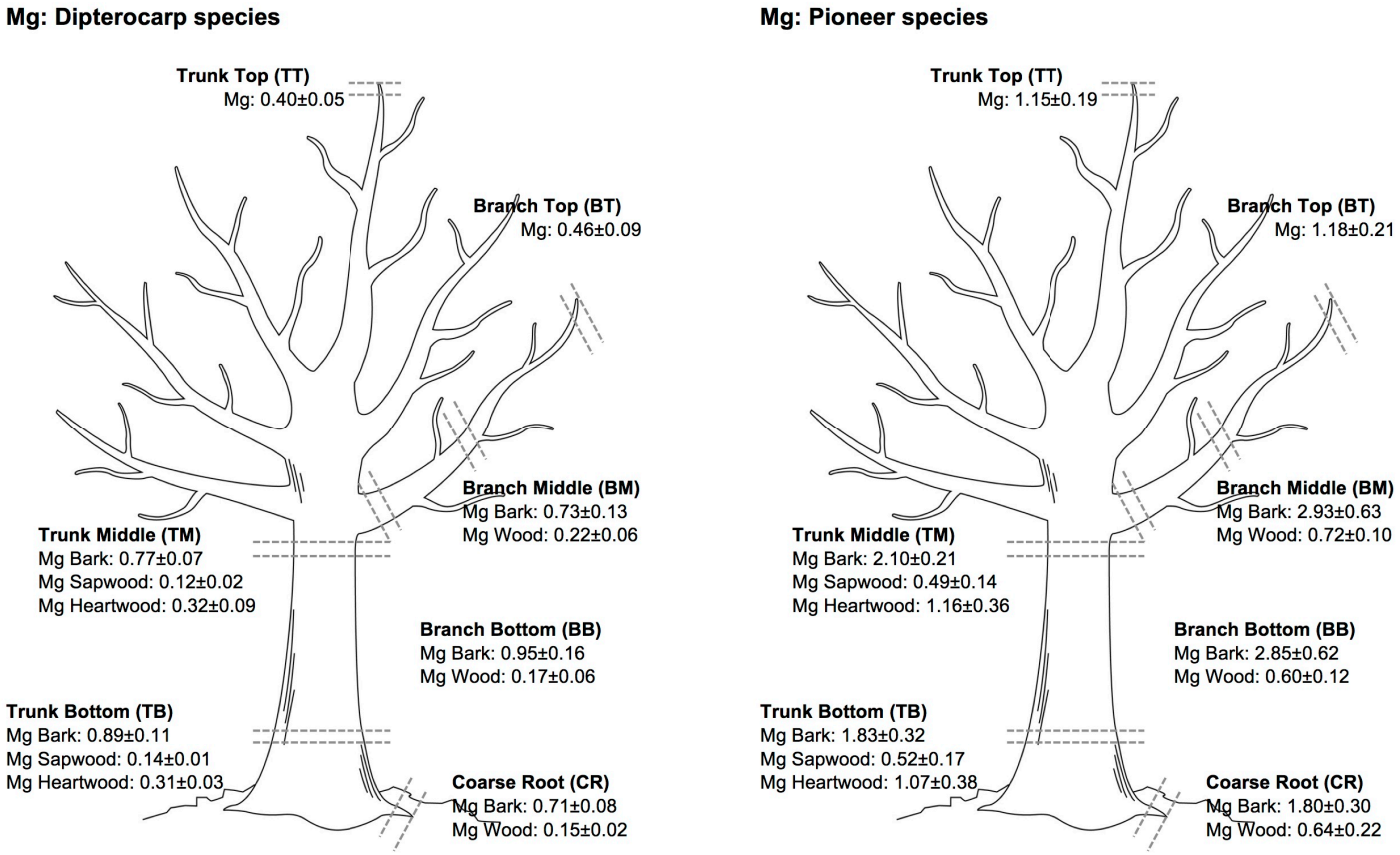


Figure 7.4 Variation of wood Mg concentrations within a whole tree of Dipterocarp and pioneer species

Values (±SE) are in mg/g, and averaged within five Dipterocarp species: *Parashorea malaanonan*, *Shorea johorensis*, *Shorea leprosula*, *Shorea micans* and *Shorea parvifolia* (*n* = 15), and within three pioneer species: *Trema orientalis*, *Macaranga pearsonii* and *Neolamarckia cadamba* (*n* = 9). Trunk samples were

partitioned to three sections: bark, sapwood and heartwood. Due to the absence of colour boundary between sapwood and heartwood in most branch and coarse root samples, they were disaggregated into wood and bark only. The tip of sampled trunk and branch was twig-like (less than 2 cm diameter), which was not debarked. See Chapter 4 for further information.

7.2 Implications

Chapter 4

Chapter 4 reports that a large amount of the nutrient capital in sapwood may be resorbed during sapwood senescence. The measurement of wood resorption requires the estimates of annual sapwood senescence and a method for separating the nutrients in the transpiration stream (which are only transiently present in the sapwood) from those that are incorporated into bulk sapwood tissue.

The results of high nutrient concentrations in bark (see Chapter 4) suggest the importance of debarking in tropical forestry. Debarking logs within the forest retains a valuable nutrient resource on site (Hilton, 1987). In some part of Sabah, Malaysia, the loss of Ca is reported substantial through timber harvesting, while total Ca in the soil is extremely low relative to the amount in biomass due to the underlying Ca-poor bedrock (Nykvist, 1997). Out study shows that roughly 80% of the K, 90% of the Ca and 60% of the Mg in an old growth forest ecosystem is in woody biomass. Hence logging of large trees represents a substantial export of these three nutrients from the system, and in the long-term repeated logging cycles may leave these ecosystems depauperate in these nutrients. Of these three nutrients, K appears the one that shows the strongest signs of limitations and could be a key limiting factor in the long term.

As another example of sustainable practices, wood ash produced in a pulp and paper mill in Sabah is returned to the forest (Nykvist, 1997). Exceptionally high bark nutrient

concentrations of all nutrient elements are reported in Chapter 4. This suggests debarking during logging operations would substantially contribute to maintaining nutrients within forest ecosystems, and could be one of the nutrient conservation practices for foresters and conservationists.

The analysis along the length of the main trunk suggests that wood sample collection near the bottom of the tree is usually representative of entire main trunk, where the bulk of woody biomass is found. Branches, however tended to show higher nutrient concentrations than the main trunk (Fig. S4.1). Sampling of outer branches may be in some cases easier and less detrimental for the tree for wood trait analyses than sampling of main trunk (e.g. when leaf traits are being collected). Given highly varied concentrations along the length of the tree, particularly among dipterocarp species (Fig. S4.1), my findings suggest that it is problematic to accurately estimate whole tree wood concentrations from branch samples.

Chapters 5 and 6

There are higher nutrient stocks in wood than that in soil for most nutrients (Fig. 7.1), which has great implications for the sustainability of logging. On the contrary, N rich soil availability implicates little evidence on N limitation.

Broader implications of understanding nutrient cycling of tropical forests include

relevance to agriculture. While P is also an essential limiting nutrient for crop yields, fertilizer derived from rock phosphate is non-renewable and expected to be in short supply in the future known as 'peak-phosphorus' (Cordell et al., 2009, Vaccari, 2009). My findings reported substantial P use efficiency in low P conditions (see Chapters 4 and 5). An understanding of how tropical plants have adapted to P limitation, either by enhancing P-use efficiency or P-uptake efficiency provides relevant information on efficient P inputs to increase crop yields while reducing P outputs from the system (Veneklaas et al., 2012).

In contrast to the low content of plant-available nutrients in the soil, the large amount of nutrients in plant biomass indicate that most nutrients are stored in biomass and less in the soil (Proctor, 1987, Whitmore, 1984), particularly as wood stock in the case of tropical forest ecosystems (Fig. 7.1). As a consequence, timber harvesting can result in great nutrient loss from forest ecosystems.

7.3 Future research

To my knowledge, resorption from fine roots has not been quantified in tropical forests, and could be estimated from a difference between nutrient concentrations of live and newly-dead fine roots. Due to data unavailability, we assumed that fine root resorption could be equivalent to leaf resorption (Fig. 7.1). A global meta analysis of plant data suggests no N resorption but substantial P resorption at the rate of 27% by fine roots

(Yuan et al., 2011). Mean resorption rates by fine roots in a subarctic flora are 27±7% for N and 57±7% for P (Freschet et al., 2010). Future research needs to address the uncertainty of fine root resorption in tropical forests. However, such research has to consider uncertainties in determining the exact period of root senescence, early decomposition of the root material (Freschet et al., 2010), and the challenge for obtaining species-specific samples in hyperdiverse ecosystems.

In addition to internal nutrient cycles (Fig. 7.1), external cycles such as atmospheric nutrient deposition and leaching need to be considered. Although site-specific data is not available, atmospheric N deposition may add 5.5–11.5 kg N ha^{-1} $year^{-1}$ (Jordan et al., 1982, Vitousek and Sanford, 1986, Schroth et al., 2001). Foliar leaching loss is reported to be < 0.5% of total N uptake, and between 1.7 and 10.9% of total P uptake in tropical trees (Hiremath et al., 2002).

Wood chemical traits need to be evaluated in concert with other functional traits such as species-level growth and mortality rates to support the conceptual framework of WES (Chave et al., 2009). It may also be necessary to examine wood chemical traits in connection with traits associate with the LES (Wright et al., 2004), if we were to fully understand whole-tree economics among co-occurring tree species across highly diverse tropical forests.

This thesis did not consider seasonal variation, which is likely to affect temporal patterns of nutrient cycling. Although no distinct seasonality exists in typical years,

ecologically significant droughts occur in the time of the El Niño in the study sites of Malaysian Borneo (Harrison, 2000, Nakagawa et al., 2000, Delissio and Primack, 2003, Potts, 2003, Ichie et al., 2004, Itioka and Yamauti, 2004). A major shift in allocation of NPP and P may occur either due to drought disturbance or after extensive masting of Dipterocarp during the El Niño (Malhi et al., 2011). Nutrient uptake by roots may also be limited by seasonal changes in soil water content (Roy and Singh, 1995). In a Brazilian Atlantic forest, nutrient inputs through litterfall vary seasonally and often peak in the middle of dry season (Villela et al., 2006). In Australian tropical forests, there is a switch between root N uptake during the wet season and N remobilisation during the dry season (Schmidt and Stewart, 1998).

A recent comprehensive review shows that there is great uncertainty and variability in how nutrient cycling responds to climate change, and overall lack of experimental data on warming effects on soil nutrient availability in tropical forests (Cusack et al., 2016). Ongoing climate change is likely to impact the way in which CO_2 and nutrients interact to limit NPP. While N availability constrains NPP of temperate plants under elevated CO_2 (Drake et al., 2011), P limitation may control the response of tropical forests to rising CO_2, if reduced transpiration rates lower P uptake (Cernusak et al., 2011). Despite this finding, experimental data on CO_2 and P interaction that limits NPP remains extremely rare (Cernusak et al., 2013). Elevated CO_2 may constrain also soil nutrient availability through changes in plant nutrient uptake, litter chemistry, decomposition rates, and soil pH which can affect weathering of rock minerals (Cusack et al., 2016).

Future research is therefore necessary to consider such climate uncertainties. One of the possibilities is to use elevation gradients as laboratories for climatic variation. For example, nutrient research can be integrated into the Andes to Amazon transect project within the Global Ecosystem Monitoring (GEM) network (Malhi et al., 2021; see http://gem.tropicalforests.ox.ac.uk) to understand the nutrient dynamics of Andean montane forests along a 2,500 m elevation gradient. As an example, a decomposition experiment using this gradient found that leaves decompose faster at higher temperatures (Salinas et al., 2011).

7.4 Concluding remarks

This thesis addresses a novel topic and substantially adds to the small amount of currently available data in the area of nutrient cycling of tropical forests. It quantified key biological processes of nutrient cycling such as nutrient requirement, uptake, use efficiency, resorption and their allocation, which have been identified as important knowledge gaps in multiple studies. Unlike previous studies that solely analyse N or P, the thesis provided the estimates of base cations as well.

It demonstrated both expected and unexpected results that have emerged in some areas. While P appears an important limiting element, other elements such as K and Ca can be also be co-limiting in some Bornean tropical forests. The magnitude of

nutrient cycling is likely to substantially vary within tropical forests due to the spatial and temporal heterogeneity of nutrient availability. Similar studies in other regions are necessary to fully understand nutrient cycling of tropical forests. As early nutrient studies suggest that tropical forests should not be categorised as a single entity (Vitousek and Sanford, 1986, Proctor, 1987), the spatial heterogeneity of wood nutrient status is expected across the tropics. The approach I have described in this thesis provides a simple and widely applicable approach that could be applied extensively across forest ecosystems.

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