Fine root dynamics and morphological traits in tropical forest ecosystems

Walter Huaraca Huasco

School of Geography and the Environment

Oriel College

University of Oxford



Supervisors:

Prof. Yadvinder Malhi, Dr. Terhi Riutta,

Dr. Cécile Girardin

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“Allin kausay kachun sachakunawan”

Thesis Summary

A major challenge in tropical belowground carbon allocation ecology is to understand how fine root dynamics and traits change across different ecosystems and environmental gradients. This study examines the spatial variation of fine root carbon stock, productivity, fractional carbon allocation of total productivity to the fine roots, and residence time across pantropical forest types. At a regional scale, this thesis investigates the vertical distribution and seasonal variation of fine root carbon stock, productivity, mortality, and residence time in lowland Amazon rainforests and Andean montane forests. In addition, this thesis examines how fine root morphological traits are related to soil properties and climatic variables from lowland to montane forests.

My first study was the largest fine root carbon stock and dynamics study across tropical forests in South America, Africa, and Southeast Asia. The analysis was carried out separately in lowland and montane forests to understand the spatial variation and the effect of soil properties and climate variables. Root dynamics were better predicted by soil properties, such as soil sand content, soil pH, and soil phosphorus content than by climatic variables, and a different set of predictors were identified for lowland and montane forests. Lower values of mean annual productivity of fine roots were observed in upper montane forests and Southeast Asian lowland forests.

My second study examined the vertical and seasonal variation in fine root dynamics in the Amazon-Andes region. The vertical distribution of fine root carbon stock and productivity in the soil profile showed proportionally more stock and productivity in the surface soil in montane forests, particularly in lower montane forests, than in lowland forests, which was related to the thickness of the organic layer. Root mortality increased in the dry season in both lowland and montane forests.

I concluded my thesis by analyzing fine root morphological traits and the root-environment relationships. These features were strongly related to soil properties and some root dynamics traits. Root tissue density emerged as the principal trait in determining the variation in root morphological traits and the rate of root foraging for resources.

This is one of the first pan-tropical studies to explore fine root dynamics along environmental gradients in neotropical and paleotropical regions. I worked with the Global Ecosystems Monitoring network teams across old-growth tropical forests ecosystems. Ultimately, my thesis provides a common analytical framework for estimating below-ground dynamics in different environmental gradients across the tropics, and the results may be used for improving global vegetation models.

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Declaration

This dissertation is the result of my own work with contribution to the experimental design, data analysis, and comments from my supervisors. The contributions of the co-authors are listed before each chapter.

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List of Acronyms

ABERG	Andes Biodiversity and Ecosystem Research Group
AFR	Africa
AIC	Akaike information criterion
$Allocation_{fr}$	Fractional allocation of total net primary productivity to the fine roots
asl	Above sea level
C	Carbon
C:N	Carbon: Nitrogen ratio
Ca	Calcium
CEC	Cation exchange capacity
CO_2	Carbon dioxide
$Cstock_{fr}$	Fine root carbon stock
CUE	Carbon use efficiency
CWD	Coarse woody debris
DE	Deviance explained
DTF	Deciduous tropical forests
ECOLIMITS	Ecosystems Limits to Poverty Alleviation in African Forest-Agriculture Landscapes
FRED	Fine-Root Ecology Database
g	Gram
GAM	Generalised additive model
GEM	Global Ecosystem Monitoring Network
Gj	Gigajoule
GPP	Gross primary productivity
ha	Hectare
IIAP	Instituto de Investigaciones de la Amazonia Peruana
INPA	National Institute of Amazonian Research
K	Potassium
kg	Kilogram
km	Kilometre
Lat.	Latitude
LEN_{fr}	Fine root length production
Long.	Longitude
MAP	Mean annual precipitation
MAT	Mean annual precipitation
MCWD	Maximum cumulative water deficit
Mg	Megagram
mg	Milligram
mm	Millimetre

mmol	Millimolar
MMP	Monthly mean precipitation
$Mortality_{fr}$	Fine root mortality
$Mortality_{fr_rh}$	Fine root mortality recorded with rhizotron technique
MTF	Montane tropical forests
N	Nitrogen
NPP	Net primary productivity
NPP_{AG}	Aboveground net primary productivity
NPP_{BG}	Belowground net primary productivity
NPP_{fr}	Fine root net primary productivity
NPP_{fr_ic}	Fine root net primary productivity recorded with ingrowth core method
NPP_{fr_rh}	Fine root net primary productivity recorded with rhizotron method
NPP_{total}	Total net primary productivity
P	Phosphorus
Pg	Petagram
Ra	Autotrophic respiration
RAINFOR	Amazon Forests Inventory Network
RMSE	Root mean square error
RTD	Root tissue density
RT_{fr}	Fine root residence time
RT_{fr_ic}	Fine root residence time recorded with ingrowth core technique
RT_{fr_rh}	Fine root residence time recorded with rhizotron technique
SA	South America
SAFE	Stability of Altered Forest Ecosystem Project
SA_{fr}	Fine root surface area production
SDTF	Semi-deciduous tropical forests
SE	Standard error
SEA	Southeast Asia
SR	Solar radiation
SRA	Specific root area
SRL	Specific root length
VOL_{fr}	Fine root volume production
WTF	Wet tropical forests
yr	year

Chapter 1: General introduction

1.1 General background

Tropical forests are crucial ecosystems that play a key function on global climate and carbon cycle. In addition, tropical forests provide free ecosystem services, including the maintenance of biodiversity, precipitation genesis, and above-belowground carbon storage. Belowground carbon stocks and fluxes are poorly studied in tropical forests. Some of the main features of the belowground carbon cycle are fine root dynamics and fine root morphological traits, which are sensitive to climate change and environmental gradients. Fine roots are defined as roots under 2 mm diameter and they grow fast, have short lifespan, and sequester more carbon in tropical forests than in temperate and boreal forests (Finér et al., 2011; Wang et al., 2018). Roots are the critical pathway for water and nutrient uptake from different soil depths, water and organic carbon transport, and also act in symbiosis with fungi to increase the uptake processes (Epron & Osawa, 2017; Gu et al., 2014; Jackson et al., 1997; McCormack & Guo, 2014). Fine root biomass and dynamics (productivity, mortality, and residence time) are key features in shaping ecosystem productivity. However, compared to above-ground biomass and productivity, fine root biomass, dynamics and their controlling factors remain poorly understood in tropical forest ecosystems. To understand the effects of rapidly changing climate and nutrient regimes on fine root dynamics in tropical forests at regional and global scales, it is important to evaluate the spatial, vertical, and seasonal variation of fine root productivity, mortality, residence time, carbon allocation, and morphological traits through long-term observations. In this thesis, I explore how environmental factors and soil nutrient content control fine root carbon stock and dynamics, what the vertical patterns of these dynamics are, how these dynamics vary seasonally, and how the choice of measurement method affects the estimates. In addition, I provide insights into the variation of fine root morphological dynamics

of total length and surface area growth and morphological traits of specific root length, specific root surface area, and root tissue density.

The total fine root dry mass per unit area is defined as *root biomass.* It is typically reported down to 30 cm and in a smaller number of studies also for deeper soil profiles. Fine root biomass is an important component of soil carbon stocks. More than 70% of fine root biomass is stored in the top 30 cm of soil depth (Jackson et al., 1997). There are currently major gaps in understanding root carbon stocks and dynamics in montane and peatland forests. However, the available estimates in tropical regions suggest that fine root carbon stock increase with elevation (e.g., Girardin et al., 2013; Moser et al., 2011; Okada et al., 2017; Sierra Cornejo et al., 2020) and with soil sand content (e.g., Jiménez et al., 2009; Kochsiek et al., 2013; Silver et al., 2000).

The dry mass of fine roots produced per unit soil surface area or unit volume per unit time is defined as *root productivity*, and *root mortality* is the dry the mass of fine roots that died per unit area or volume per unit time (Freschet et al., 2020)**.** Root productivity is a key feature for understanding the effect of soil properties and climate on the ecosystem carbon dynamics, due to the interconnected nature of the aboveground and belowground carbon cycles. In montane forests, the variation in root productivity with elevation is poorly understood, some studies reporting a decrease (e.g., Girardin et al., 2013; Sierra Cornejo et al., 2020) and others an increase with elevation (e.g., Moser et al., 2010; Röderstein et al., 2005). These inconsistent results may be due to different methods and sampling biases, with root productivity overestimated or underestimated in highly organic and acidic soils.

Fine root productivity divided by total net primary productivity is defined as the *fractional allocation* of total net primary productivity to the fine root structures. This feature can greatly increase our understanding the functioning of the belowground ecosystem and carbon allocation, but it has rarely been well quantified, because of the need for measuring not

only roots but also the components of aboveground productivity (Malhi et al., 2011). Under soil nutrient limitations, plants may benefit from a strategy to allocate more carbon into fine roots to increase water and nutrient uptakes.

The ratio of root biomass and productivity is *root residence time* and this ratio increases with latitude from tropical to boreal forests (Finér et al., 2011; Gill & Jackson, 2000; Joslin et al., 2006) and with elevation from lowland to montane forests (Girardin et al., 2013; Okada et al., 2017).

Fine root morphological traits provide insights into root strategies and root-environment relationships (Assefa et al., 2017; Maeght et al., 2015; Silver et al., 2005). The most common root morphological traits are: diameter, length growth, surface area growth, specific root length, specific root surface area, and root tissue density. Studies of these traits in tropical regions are beginning to reveal the relationships between traits and soil resources, and their linkages with fungal symbionts (Iversen, 2014; Li et al., 2019).

Most tropical fine root dynamics studies employ the ingrowth core technique. This method was suggested to be used with caution in forests with slow root growth (Addo-Danso et al., 2016), because root biomass may be affected by strong seasonal variation and the timing of sampling (Katayama et al., 2019), and in water saturated soils. Other techniques are becoming more common. For example, minirhizotron tubes with an automatic scanner to scan roots at different soil depths has been used in montane forests (Graefe et al., 2008; Moser et al., 2010) and in lowland forests (Cordeiro et al., 2020; Wright et al., 2011).

In the context of belowground ecology, my thesis will help to understand different aspects of fine root dynamics and morphological traits across tropical forests, with long-term datasets that have been collected from neotropical and paleotropical forests. In addition, root morphological traits data at 0.1 mm diameter classes provides information on how soil properties and climate control root morphological variation. The results of this thesis have a

key role to play in informing current global ecosystems models to refine estimates on how these important ecosystems will respond to climate change.

1.2 Aims

The main objective of this DPhil thesis was to examine the global and regional variation and the effect of soil properties and climatic variables on fine root carbon stock, productivity, residence time, fractional allocation of productivity to fine roots, and morphological traits in tropical old-growth forest ecosystems. This study presents data from forty-seven forest plots in lowland and montane tropical forests in South America, Africa, and Southeast Asia, where fine root dynamics, soil properties and total net primary productivity data were collected using standardised protocols across all sites. The data and findings from this study increase our understanding of belowground carbon cycling across the pantropics and contributes towards a better overall understanding of total ecosystem carbon dynamics. Specifically, I address the following research questions:

- *What are the common environmental factors that explain fine root dynamics, and is there a single unified model of fine root dynamics across tropical forest ecosystems?*
- *How does fine root productivity and mortality vary both seasonally and vertically along the soil profile in Amazonian and Andean forests?*
- *How are fine root morphological traits affected by soil nutrient content and environmental factors across different root diameter categories?*

1.3 Outline of the thesis

Chapters 1 and 2 provide an introduction and literature review of the research theme, respectively. Chapter 3 provides site description and methods.

Chapters 4, 5 and 6 are the empirical chapters. They are three independent but interlinking studies, which have been submitted as scientific papers to peer-reviewed journals.

The first empirical chapter is "*Fine root dynamics across pantropical rainforest ecosystems*" (Chapter 4). This chapter provides one of the largest quantifications of pantropical fine root dynamics (fine root stock, productivity, residence time and fractional allocation of net primary productivity to fine roots) and their relationship to soil and climatic factors, covering three continents and lowland and montane forests.

The second empirical chapter describes the "*Vertical and temporal variation of fine root dynamics in Amazonian and Andean forests"* (Chapter 5), spanning semi-deciduous, wet, and montane forest ecosystems in three South American countries of Bolivia, Brazil, and Peru. This chapter examines the vertical distribution of fine root carbon stocks, productivity, and mortality in the soil profile, and the seasonal variation of root productivity and mortality. Furthermore, this paper compares the ingrowth core and rhizotron techniques.

The third empirical chapter **"***Fine root morphological traits along an elevation gradient in Amazonia-Andean tropical rainforests"* (Chapter 6), is the largest tropical study to date of belowground traits and their relationship with soil nutrient content and climatic variables, recorded by 0.1 mm root diameter classes from upper montane to lowland forests of Peru.

Chapter 7 provides the closing conclusions of this DPhil thesis, synthesising the from three papers that provide probably the largest in-depth analysis of fine root dynamics and morphological traits across lowland forests and montane tropical forests.

1.4 References

Addo-Danso, S. D., Prescott, C. E., & Smith, A. R. (2016). Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. *Forest Ecology and Management*, *359*, 332–351. https://doi.org/10.1016/j.foreco.2015.08.015

Assefa, D., Rewald, B., Sandén, H., & Godbold, D. L. (2017). Fine Root Dynamics in Afromontane Forest and Adjacent Land Uses in the Northwest Ethiopian Highlands. *Forests*, *8*(7), 249. https://doi.org/10.3390/f8070249

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde-Barrantes, O., Fuchslueger, L., Oblitas, E., … Quesada, C. A. (2020). Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant-Environment Interactions*, *1*(1), 3–16. https://doi.org/10.1002/pei3.10010

Epron, D., & Osawa, A. (2017). Fine roots: when anisotropy matters. *Tree Physiology*, *37*(6),

693–696. https://doi.org/10.1093/treephys/tpx063

Finér, L., Ohashi, M., Noguchi, K., & Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management*, *262*(11), 2008–2023. https://doi.org/10.1016/j.foreco.2011.08.042

Freschet, G., Pagès, L., Iversen, C., Comas, L., Rewald, B., Roumet, C., … Postma, J. (2020). A starting guide to root ecology: Strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements, (August).

Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, *147*(1), 13–31. https://doi.org/10.1046/j.1469-8137.2000.00681.x

Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082

Graefe, S., Hertel, D., & Leuschner, C. (2008). Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil*, *313*(1–2), 155–166. https://doi.org/10.1007/s11104-008-9688-z

Gu, J., Xu, Y., Dong, X., Wang, H., & Wang, Z. (2014). Root diameter variations explained by anatomy and phylogeny of 50 tropical and temperate tree species. *Tree Physiology*, *34*(4), 415–425. https://doi.org/10.1093/treephys/tpu019

Iversen, C. M. (2014). Using root form to improve our understanding of root function. *New Phytologist*, *203*(3), 707–709. https://doi.org/10.1111/nph.12902

Jackson, R. B., Mooney, H. A., & Schulze, E. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(14), 7362–7366. https://doi.org/10.1073/pnas.94.14.7362

Jiménez, E. M., Moreno, F. H., Lloyd, J., Peñuela, M. C., & Patiño, S. (2009). Fine root dynamics for forests on contrasting soils in the colombian Amazon. *Biogeosciences Discussions*, *6*(2), 3415–3453. https://doi.org/10.5194/bgd-6-3415-2009

Joslin, J. D., Gaudinski, J. B., Torn, M. S., Riley, W. J., & Hanson, P. J. (2006). Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. *New Phytologist*, *172*(3), 523–535. https://doi.org/10.1111/j.1469-8137.2006.01847.x

Katayama, A., Kho, L. K., Makita, N., Kume, T., Matsumoto, K., & Ohashi, M. (2019). Estimating Fine Root Production from Ingrowth Cores and Decomposed Roots in a Bornean Tropical Rainforest. *Forests*, *10*(1), 36. https://doi.org/10.3390/f10010036

Kochsiek, A., Tan, S., & Russo, S. E. (2013). Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology*, *214*(6), 869–882. https://doi.org/10.1007/s11258-013-0215-9

Li, F., Hu, H., McCormlack, M. L., Feng, D. F., Liu, X., & Bao, W. (2019). Community-level economics spectrum of fine-roots driven by nutrient limitations in subalpine forests. *Journal of Ecology*, *107*(3), 1238–1249. https://doi.org/10.1111/1365-2745.13125

Maeght, J., Gonkhamdee, S., Clément, C., Isarangkool Na Ayutthaya, S., Stokes, A., & Pierret, A. (2015). Seasonal Patterns of Fine Root Production and Turnover in a Mature Rubber Tree (Hevea brasiliensis Müll. Arg.) Stand- Differentiation with Soil Depth and Implications for Soil Carbon Stocks. *Frontiers in Plant Science*, *6*, 1022. https://doi.org/10.3389/fpls.2015.01022

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1582), 3225–3245. https://doi.org/10.1098/rstb.2011.0062

McCormack, M. L., & Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science*, *5*, 205. https://doi.org/10.3389/fpls.2014.00205

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., & Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*, *17*(6), 2211–2226. https://doi.org/10.1111/j.1365-2486.2010.02367.x

Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., & Hertel, D. (2010). Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity*, *3*(2), 151–164. https://doi.org/10.1080/17550874.2010.517788

Okada, K., Aiba, S., & Kitayama, K. (2017). Influence of temperature and soil nitrogen and phosphorus availabilities on fine-root productivity in tropical rainforests on Mount Kinabalu, Borneo. *Ecological Research*, *32*(2), 145–156. https://doi.org/10.1007/s11284-016-1425-0

Quesada, C. A., Paz, C., Oblitas Mendoza, E., Phillips, O., Saiz, G., & Lloyd, J. (2020). Variations in soil chemical and physical properties explain basin-wide variations in Amazon forest soil carbon densities. *Soil*, 1–62. https://doi.org/10.5194/soil-6-53-2020

Röderstein, M., Hertel, D., & Leuschner, C. (2005). Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, *21*(5), 483–492. https://doi.org/10.1017/S026646740500249X

Sierra Cornejo, N., Hertel, D., Becker, J. N., Hemp, A., & Leuschner, C. (2020). Biomass, Morphology, and Dynamics of the Fine Root System Across a 3,000-M Elevation Gradient on Mt. Kilimanjaro. *Frontiers in Plant Science*, *11*, 13. https://doi.org/10.3389/fpls.2020.00013

Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., & Cosme, R. (2000). Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. *Ecosystems*, *3*(2), 193–209. https://doi.org/10.1007/s100210000019

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., … Keller, M. (2005). Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology*, *11*(2), 290–306. https://doi.org/10.1111/j.1365-2486.2005.00903.x

Wang, C., Chen, Z., Brunner, I., Zhang, Z., Zhu, X., Li, J., … Li, M.-H. (2018). Global patterns of dead fine root stocks in forest ecosystems. *Journal of Biogeography*, *45*(6), 1378–1394. https://doi.org/10.1111/jbi.13206

Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., … Corre, M. D. (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, *92*(8), 1616–1625. https://doi.org/10.1890/10-1558.1

Chapter 2: Literature review



San Pedro and Tono buffer zones of Manu National Park in Peruvian lower montane and pre-montane forests (left panels) and overview of Trocha Union cloud forest and sunrise in Kosñipata Valley, Peru (right panels).

2.1 Tropical forest ecosystems and anthropogenic drivers

Tropical rainforests are complex and megadiverse ecosystems, distributed across the pantropical region covering 44% to 48% of the global land area (Keenan et al., 2015; Potapov et al., 2017). Tropical forest areas are under chronic pressure from climatic change and anthropogenic activities. Old-growth tropical forest area has been decreasing progressively, due to wood harvest increasing from a minor to a major driver from 1900 to present (McDowell et al., 2020). Today, approximately 75% of the original, pre-industrial tropical forest area remains, of which approximately 30% is intact forests (Keenan et al., 2015; Potapov et al., 2017). In the recent decades, between 1990 and 2015, a larger proportion of tropical forest than boreal or temperate forest has been converted into other land use types (Food and Agriculture Organisation 2015). Keenan et al. (2015) reported that the total area of tropical forests declined at a rate of 5.5 million hectares per year between 2010 and 2015, and the net loss of tropical forest area over the last five years was largest in Brazil (0.98 million hectares per year), Indonesia (0.68 million hectare per year), and Nigeria (0.41 million hectare per year). The net loss rate has decelerated from 8.0 million ha per year in the 1990s and 7.6 million ha per year in the 2000s. Tropical forest deforestation and degradation are major sources of carbon emissions, of which deforestation accounts for 75% or 6.22 Gt CO_2e $year^{-1}$ and degradation accounts for 25% or 2.06 Gt CO_2e $year^{-1}$, respectively (Pearson et al., 2017).

Tropical forest ecosystems are major stores of both above and belowground carbon and they form approximately 40% of the terrestrial ecosystem carbon sink; however, their ability to sequester carbon into biomass is declining (Hubau et al., 2020). Increasing atmospheric CO_2 concentration, increasing temperature, drought events with hydrological changes, and changes in forest dynamics have been driving the long-term decline of aboveground biomass across the tropics. By 2030 the carbon sink in aboveground live biomass in African old-growth forests is

predicted to decline by 14%, whereas in the Amazonian forest it is predicted to decline even more rapidly, reaching zero in 2035 (Brienen et al., 2015; Hubau et al., 2020).

A study on the thermal sensitivity of tropical forest carbon dynamics show that maximum temperature is the most important predictor of aboveground biomass stock across the tropics, and the negative effect of daytime maximum temperature on aboveground biomass stock is the main driver of the decline in woody productivity (Sullivan et al., 2020). On the other hand, the proportion belowground biomass is predicted to increase in montane forests and dry forests under warmer temperatures to enhance the uptake of water and nutrients, which are scarce in such environments (Reich et al., 2014).

Drought events produce negative effects for tropical forests, reducing C uptake by decreasing photosynthesis and autotrophic respiration (Brando et al., 2019). Across tropical forests, the last El Niño (1997/9 and 2015/18) had a weak impact in Africa but a strongly negative impact in parts of Southeast Asia and in extensive regions across central and eastern Amazonia, with decrease in wood growth (Rifai et al., 2018). Amazon forests experienced strong drought events in 2005 and 2010, and during these periods, trees prioritized growth by reducing autotrophic respiration especially in roots and stems (Doughty et al., 2015). The Amazon region lost 0.48 peta-grams of carbon per year between 2010 and 2011 due to drought, highlighting that moisture has a pivotal role in determining the Amazonian carbon balance (Gatti et al., 2014). Some drought events across tropical regions are severe with extreme heat that was registered between 2014 and 2017 and the aboveground carbon stock component decreased by 1.3 Pg C (Wigneron et al., 2020).

2.2 Tropical lowland old-growth forests

Lowland tropical forests span wet or evergreen rain forests, semi-deciduous, and dry deciduous or seasonally dry forests (Malhi & Grace, 2000). The largest tropical lowland forest areas are located in the Amazon basin, followed by African and Asian forests, however the annual

deforestation in Southeast Asia is the highest among all tropical regions and it has increased between 1990-2000 and 2000-2005 (Aleman et al., 2018). By 2100, the Asian forests will lose between 10-85% of biodiversity because less than 10% of forests are under some form of protection (Sodhi et al., 2010).

Lowland tropical forest soils are old and highly weathered with low availability of phosphorus (P), nitrogen (N), potassium (K) and other cations (Goldstein, 2016; Yuan et al., 2011). P is the most limiting element, the acquiring of which has a high carbon cost in tropical forests; three times higher than in temperate forests (Allen et al., 2020; Du et al., 2020). The mean annual temperature ranges between 24 and 34 ^{o}C in lowland tropical forests (Sayre et al., 2020). Pantropical estimates of the mean carbon stock across lowland forests, based on a dataset of 360 one-hectare plots range between 140 and 197 Mg C ha^{-1}, with the highest mean storage in Asian forests (Sullivan et al., 2017).

Lowland tropical forests can be further divided into moist forests, semi-deciduous forests and dry or deciduous forest (Feng et al., 2013; Rifai et al., 2018) based on their rainfall and vegetation.

2.2.1 Tropical moist forests

Lowland evergreen forests or rainforests are dense ecosystems in pantropical regions with a wet climate, without pronounced dry seasons. The annual precipitation is greater than ~ 2000 mm (Pennington et al., 2018). Tropical rainforests have closed, tall canopies typically over 25 m, but may reach over 50-70 m in some regions (Pennington et al., 2018).

The evergreen Amazon rainforest is the largest lowland rainforest ecosystem that spans eight South American countries. In Amazon forest, eight vegetation formations have been described to date: swamp forest or Pastaza, bamboo-dominated forest, white-sand forest, turnover zone between the Solimões and Içá formations, sandy megafan formations in Roraima, and the Brazilian and Guiana Precambrian shield (Tuomisto et al., 2019). Across

these vegetation formations 11676 tree species have been described and collected to date, Brazil harbouring the largest number of tree species (7694), followed by Peru (Ter Steege et al., 2019). However, this richness of tree species across Amazonia may be affected by climate change with increasing tree mortality of short-lived species pioneers, softwoods, and evergreens during the droughts, storms and extreme rainy events (Aleixo et al., 2019).

The largest African lowland rain forest area is located in the Central Africa (~1784473 km^2) that spans terra firme wet and peatland forest ecosystems, followed by West Africa (~119897 km^2), Eastern Africa (~47959 km^2), and Madagascar (~43962 km^2) (Malhi et al., 2013). The Ice Ages caused expansion of savannahs and contraction of the rainforest in Central African regions where high numbers of endemic species have been reported (Piñeiro et al., 2017). The Congo basin forest receives less precipitation annually than Amazon region and Southeast Asia forest (Malhi, 2018).

The Southeast Asian rainforests ecosystems may rival or exceed the Amazon forests in tree species richness. These forests are dominated by the single family of Dipterocarpaceae with 510 species reported across the Southeast Asian islands (Kettle, 2010). The climate is primarily driven by monsoon winds (Gathorne-Hardy et al., 2002; Kooyman et al., 2019). Borneo island is the second largest island in Southeast Asia after New Guinea and has lost ~ 465 000 km^2 its old-growth forest since the 1970s, replaced by large-scale industrial oil palm plantations (Jucker et al., 2018). Palm oil production in Borneo island is associated with annual forest loss and has been increasing by 9% every year (Gaveau et al., 2019; Uning et al., 2020).

2.2.2 Tropical semi-deciduous forests

Semi-deciduous tropical forests are transitional forests between moist and dry forests, and these transitional forests are shaped by rainfall, species phenology, soil properties, and temperature (Pennington et al., 2018). In African tropical semi-deciduous forests, the monthly precipitation presents a bimodal pattern across the year. The western African region experiences two rainy

seasons, the first between March and June and the second between September and October, and dry months between December and February. Old-growth forests of Kakun National Park, Bepo, and Bobiri Forest Reserves have a mean annual precipitation between ~1288 mm and 1500 mm (Addo-Danso et al., 2018; Baker et al., 2003; Moore et al., 2018; Pappoe et al., 2010). The annual precipitation is high in central African semi-deciduous forests, ranging between 1500 mm and 1800 mm in Congo basin countries of Central African Republic, Cameroon, and Gabon (Deans et al., 1996; Freycon et al., 2015; Wade et al., 2019). The mean annual temperature in western and central African semi-deciduous forests range between 25 ^{o}C and 25.7 ^{o}C (Moore et al., 2018; Wade et al., 2019). Congo basin semi-deciduous old-growth forests grow on Ferrasols and Cambisols (Freycon et al., 2015; Wade et al., 2019) and western semi-deciduous forest growth on Acrisols (Addo-Danso et al., 2018; Pappoe et al., 2010).

In the Amazon basin the semi-deciduous forests area covers 142100 km^2 (Eva et al., 2004). The rainy season is between October and March, and the dry season between April and September. The Brazilian semi-deciduous forests have an annual precipitation of 1400 mm to 2000 mm and annual temperature of 24^{o}C to 25^{o}C. These forests grow on Alluvium Gleysols and Ferrasol (Marimon et al., 2014; Rocha et al., 2014; Vourlitis et al., 2008).

2.2.3 Tropical dry or deciduous forests

Tropical dry forests are defined as a deciduous ecosystem with marked seasonality and closed canopies, and grow on fertile soils (Banda et al., 2016; Moonlight et al., 2020; Powers et al., 2015). Dry forest ecosystems have been poorly studied regarding their carbon storage, productivity, water cycle, and other biogeochemical cycling, and the monitoring of these variables is still in its infancy (Moonlight et al., 2020; Pennington et al., 2018). In tropical regions, 42% of the area is covered by dry forests, making them the second most important forest type after moist forests (Hasnat & Hossain, 2020; Van Bloem et al., 2004).

In South America, 60% of the dry forests have been destroyed by conversion to croplands and other land uses, and dry forests also constitute the main source of fuelwood and charcoal (Hasnat & Hossain, 2020). Half of the global dry forest area is located in South America (Miles et al., 2006), and the ~ 23000 km^2 surface area is under legal protection in Bolivia and Brazil. Chiquitano dry forest region is the largest ecosystem of Bolivia that covers an area of 7600 km^2, dry forests in Brazil cover an area of 81046 km^2 with a protected area of 5015 km^2, and only 1.2 % of the total Caatinga dry forest in Brazil is fully protected (Portillo-Quintero & Sánchez-Azofeifa, 2010). Across the neotropical dry forest regions the mean annual precipitation ranges between 700 mm and 1800 mm and temperature is above 25^oC (Banda et al., 2016; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa et al., 2005).

African dry forests are characterised by relatively poor forest protection and unsustainable management, and the two main centres of dry forests are located in western Ethiopia, southern Sudan and Mozambique (Bodart et al., 2013; Miles et al., 2006). In western Africa, dry forests have been converted to cropland and scrubland. The mean annual precipitation in western African regions ranges between 800 mm and 1200 m, and the mean annual temperature is above 26^oC (Ibrahim et al., 2020; Moore et al., 2018; Ouedraogo et al., 2011).

2.3 Tropical montane forests

Tropical montane forests are hotspots of many endemic species, constitute carbon reservoirs and provide hydrological services for tropical regions (Adhikari et al., 2020; Soh et al., 2019; Spracklen & Righelato, 2014). Climatic variables, predominantly temperature, precipitation, humidity, solar radiation and micro-climate, and soil properties change drastically with elevation in montane forests (Bendix et al., 2013). Montane forests are distributed between 500 m asl and ~ 3500 m asl and represent 0.26% of the earth land surface area across 41 countries

(Bubb et al., 2004). The global surface area of tropical montane forests is ~1.2 million km^2 (Spracklen & Righelato, 2014) and the largest area is located in Asia that represents 43.2% of the total tropical montane forest area (Scatena et al., 2010).

Scatena et al. (2010) classified tropical montane forests into lower, upper, and sub-alpine montane (dwarf forests) forest types. As elevation increases in montane forests the tree height gradually decreases, and moss cover on stems increases from 10% to 80%. Tree height ranges between 15 m and 35 m in lower montane, 1.5 m and 8 m in upper montane, and 1.5 and 9 m in sub-alpine montane forests (Bruijnzeel et al., 2011). Pre-montane forests, also called middle elevation forests, are located between 500 and 1500 m. The mean annual temperature in the montane forests ranges between 23.5^{o}C (595 m asl) and 9.0^{o}C (3537 m asl) in the Peruvian Kosñipata Valley (Blonder et al., 2017; Malhi et al., 2017). The mean annual precipitation varies according to montane forest types. In Peru, the precipitation is lowest, 1560 mm yr^{-1}, in upper montane forest (Girardin et al., 2014), and highest, 5302 mm yr^{-1}, in lower montane forest.

2.4 Net primary productivity and carbon cycle in tropical forest ecosystem

Organic carbon cycle in forest ecosystems begins when plants assimilate atmospheric carbon dioxide and convert it into carbohydrate molecules by photosynthesis pathway (Equation 2.1, Figure 2.1). The atmospheric uptake of CO_2 through photosynthesis is defined as gross primary productivity (GPP), and the total net primary productivity (NPP) is defined as the difference between GPP and autotrophic respiration (Ra). The ratio of NPP to GPP is called carbon use efficiency (CUE), which averages ~ 30% in old-growth tropical forests (Malhi et al., 2011). Hence, ~ 70% of carbon assimilated by plant photosynthesis returns to the atmosphere through the autotrophic respiration from leaves, reproductive organs, branches, stem, and root tissues (Malhi et al., 2015). The remaining carbon is allocated to building new organic tissue of

aboveground (leaf, flowers, fruits, branches, stem) and belowground (coarse roots, fine roots) components of NPP (Malhi et al., 2011; Marthews et al., 2012).

$$6CO_2 + 6H_2O \xrightarrow{\text{Solar energy}} C_6H_{12}O_6 + 6O_2 \quad (2.1)$$

$$NPP = GPP - Ra \quad (2.2)$$

$$CUE = NPP / GPP \quad (2.3)$$

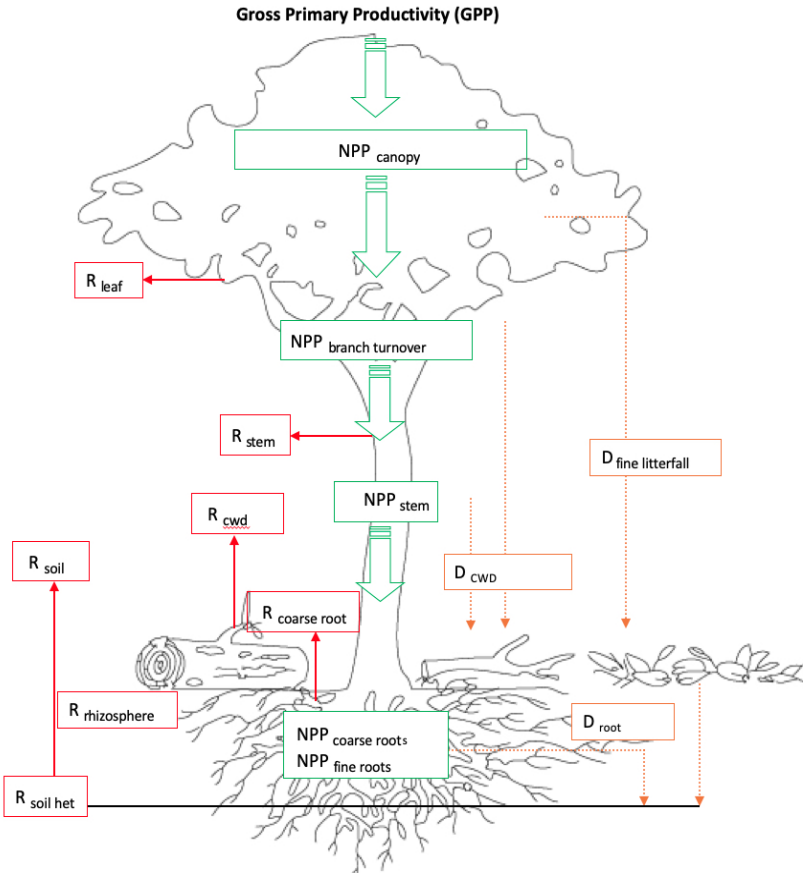


Figure 2.1. Carbon cycle in a forest ecosystem, showing gross primary productivity (GPP), net primary productivity (NPP) and its allocation into aboveground (NPP_{canopy}, $NPP_{branch\ turnover}$, NPP_{stem}) and belowground ($NPP_{coarse\ roots}$, $NPP_{fine\ roots}$) components, autotrophic respiration (R_{leaf}, R_{stem}, $R_{rhizosphere}$), heterotrophic respiration (R_{CWD}, $R_{soil\ het}$), and production of organic detritus (D_{CWD}, $D_{fine\ litterfall}$, D_{root}). CWD – coarse woody debris. Adapted from Malhi et al. (2014).

2.4.1 Aboveground net primary productivity (NPP_{AG})

Tropical forest ecosystems and savannas account for over 60% of global terrestrial gross primary productivity (photosynthesis) making them a key element in the global carbon cycle (Malhi et al., 2014a). Approximately 30-50% of the GPP is used for net primary productivity (NPP), allocated to the production of leaves (NPP_{leaf}), flowers (NPP_{flower}), fruits (NPP_{fruit}), woody productivity over 10 cm and under 10 cm diameter ($NPP_{ACW\geq 10\ cm}$, $NPP_{ACW<10\ cm}$), coarse roots ($NPP_{coarse\ roots}$), and fine roots ($NPP_{fine\ roots}$) (Marthews et al., 2012).

A pantropical carbon allocation study revealed that on average 73% of carbon is allocated to NPP_{AG} (Malhi et al., 2011). Regional estimates range from 59% in montane forests

above cloud base immersion zone in the Peruvian Andes (Girardin et al., 2014; Huaraca Huasco et al., 2014), 63% to 72% in Eastern Amazon (Doughty et al., 2014), 75% to 82% in western Amazon (del Aguila-Pasquel et al., 2014; Malhi et al., 2017), and approximately 81% in Malaysian Borneo (Kho et al., 2013). NPP_{AG}, in turn, may be invested into woody and canopy production in differing proportions. Precipitation gradient across deciduous forests, semi-deciduous forests and savannas in Western Africa shows between 50% to 60% allocation of NPP_{AG} to canopy production (Moore et al., 2018), while old-growth forests in Borneo allocate 48% and 42% to canopy and woody production respectively (Riutta et al., 2018). NPP_{AG} allocation may also show seasonality, with high allocation to canopy in the dry season (Doughty et al., 2015). A recent study reported that above and belowground carbon allocation under drought events depended on soil properties, with increasing fine root productivity on sandy soil and increasing litterfall and wood growth on clay soil forests (Jiménez et al., 2020).

$$NPP_{AG} = NPP_{ACW\geq 10cm} + NPP_{ACW<10\ cm} + NPP_{branch\ turnover} + NPP_{canopy} \quad (2.4)$$

2.4.2 Belowground net primary productivity (NPP_{BG})

Fine roots perform the key function of water and nutrient uptake, and they are a major component of the NPP_{BG}. Despite their importance, fine roots have been less studied than the aboveground components, and there is no consensus on which techniques are the best ones to study root dynamics (Addo-Danso et al., 2016; Drewniak, 2019). Malhi et al., (2011) reported a mean fractional allocation of 27% of the net primary productivity to the fine roots for the pantropics, however this fraction varies across sites depending on their environmental conditions and soil properties. A seasonal study of root carbon allocation reported an increase in wet season from Andes to lowland Amazon forests with the highest fraction of 48% in lowland wet forests during the wet season (Doughty et al., 2015). In moist forest in Malaysia

Borneo, fractional allocation of NPP to fine roots was 18% (sandy soil) and 20% (clay soil) for Malaysian Borneo moist forests (Kho et al., 2013). In Amazon, there was a positive relationship between soil sand content and carbon allocation to the fine roots (Castanho et al., 2013). Therefore, tropical plants adopt strategies for nutrient and water uptake with increasing carbon allocation to the fine roots when the resources as scarce (Sierra Cornejo et al., 2020).

$$NPP_{BG} = NPP_{\text{fine root}} + NPP_{\text{coarse root}} \quad (2.5)$$

2.5 Ecology and carbon dynamics of fine roots

In this study, fine roots were defined using the traditional diameter threshold of ≤ 2 mm reported by many previous ecosystem carbon dynamics studies in tropical montane forests (e.g., Girardin et al., 2013; Moser et al., 2011; Okada et al., 2017; Röderstein et al., 2005; Sierra Cornejo et al., 2020) and tropical lowland forests (e.g., Jackson et al., 1997; Kho et al., 2013; Moore et al., 2018; Riutta et al., 2018). Fine roots perform the belowground ecosystem processes of nutrient and water uptake, and symbiosis with mycorrhizal fungi (Iversen et al., 2017). Fine roots contribute large C inputs into the soil through root exudates, production, and necromass (Germon et al., 2020). For a better understanding of fine root traits variation within and among plant species fine roots have been grouped into two functional categories: long-lived transport roots and short-lived, most distal absorptive fine roots, which are involved in nutrient uptake and may change their morphological traits according to their fungal associations (McCormack et al., 2015, 2017). Recently, Laliberté (2017) proposed new belowground frontiers in trait-based ecology, including the separation of fine roots into absorptive and transport components and the determination of root trait variation across environmental gradients.

In tropical forest ecosystems, fine root carbon stock down to 30 cm soil depth accounts for between 42% and 57% of the total fine root carbon stock (Cordeiro et al., 2020; Jackson et

al., 1997). Between 20-30% of total root carbon stock is stored in the top 10 cm soil depth (Telles et al., 2003). Tropical forests accumulate a greater root carbon stock compared with temperate and boreal regions (Wang et al., 2018) and root carbon stock is higher in montane forests than in lowland forests (Cavelier, 1992; Ibrahima et al., 2010). Root carbon stock across old-growth tropical forest ecosystems in the Amazon basin, Congo basin (Central Africa), and in the remaining Southeast Asian forests still constitute a knowledge gap, because most carbon budgets studies have focussed on aboveground components. Furthermore, most fine root carbon stock studies in tropical old-growth forests have quantified the stock in the top soil profile (≤ 30 cm), but less information is available on deep roots.

Soil nutrient content and climate variables are key factors determining fine root carbon stocks in tropical forests. Globally, ~30% of the variation in root carbon stock can be predicted by soil texture and climatic variables (Cusack et al., 2018). Root carbon stock decreases with increasing soil K and P (Espeleta & Clark, 2007; Silver et al., 2000; Yavitt et al., 2011), but increases with increasing N, C:N ratio and N:P ratio (Espeleta & Clark, 2007; Leuschner, Moser et al., 2007; Moser et al., 2011, 2010; Zhu et al., 2013). Root carbon stock in lowland forests is positively related to soil sand content (Cavelier, 1992; Metcalfe et al., 2008; Silver et al., 2005; Tanner et al., 1998). In addition, the vertical distribution of the fine root carbon stock is negatively related to soil acidity and declines exponentially with vertical profile of soil nutrients (Adamek et al., 2011; Campos et al., 2017; Hertel et al., 2009; Leuschner et al., 2006). Soil organic layer is preferred by fine roots due to its higher nutrient availability, therefore, the root carbon stock in the organic layer is typically high (Hölscher et al., 2009; Soethe et al., 2006). In montane forests, root carbon stock in the organic layer may constitute between 48% (pre-montane) to 75% (upper montane) of the total root carbon stock (Hölscher et al., 2009; Soethe et al., 2006), as the organic layer thickness increases with increasing elevation.

The main climatic factor that drives root carbon stock in lowland forests is the mean annual precipitation, which is positively correlated with root biomass across rainfall gradient from dry to moist forests (Cavelier et al., 1999; Cusack et al., 2018; Ibrahim et al., 2020). In montane forests, on the other hand, temperature is the main driver of root carbon stock, with a positive relationship (Moser et al., 2011; Okada et al., 2017). Precipitation has been found to have a unimodal relation with root biomass in some montane forests, with a peak at ~ 2000 m (Sierra Cornejo et al., 2020).

Fine root productivity in tropical lowland forests decreases at community level with soil fertilization of N and K (Peng et al., 2017; Wright et al., 2011; Wurzburger & Wright, 2015; Yavitt et al., 2011; Zhu et al., 2013). The addition of P, on the other hand, increases fine root productivity (Wright et al., 2011; Yuan & Chen, 2012; Zhu et al., 2013). C:N ratio (Valverde-Barrantes et al., 2007) and soil sand content (Jiménez et al., 2009; Kochsiek et al., 2013; Silver et al., 2005) are also positively related to fine root productivity. Annual variation in fine root growth is driven by annual precipitation, with a positive relationship recorded in different lowland tropical forest sites across the pantropics (Cordeiro et al., 2020; Green et al., 2005; Ibrahim et al., 2020; Kho et al., 2013). Fine root productivity in tropical montane forests, fine root productivity is positively related to soil C:N ratio and soil acidity in Ecuador (Moser et al., 2010) and in Tanzania (Sierra Cornejo et al., 2020) while fine root productivity is negatively related to N and positively related to P in Borneo (Okada et al., 2017). The main climatic driver in tropical montane forest may vary between different tropical regions. In Africa, mean annual precipitation was positively related to root productivity (Sierra Cornejo et al., 2020), while in South America (Girardin et al., 2013; Moser et al., 2010) and in Southeast Asia (Okada et al., 2017), the mean annual temperature was also positively related to root productivity.

Studying seasonality in fine root dynamics is challenging, because it requires sampling at high temporal frequency. Therefore, data on seasonal fine root dynamics in tropical forests is limited. Seasonal productivity of fine roots in tropical lowland forests is related to monthly precipitation, with increased productivity in the rainy season (Andrade, Rosa, Almeida, Silva, & Sena, 2020; Araujo-Murakami et al., 2014; Malhi et al., 2014b; Sánchez-Gallén & Alvarez-Sánchez, 1996).

Information on the vertical patterns of fine root productivity (rather than stock) is very limited in tropical forests. The available studies reported between 70% and 80% of fine root growth in the first 10 cm soil depth (Ibrahima et al., 2010) and 60% within the top 30 cm soil depth (Cordeiro et al., 2020).

Fine root mortality and productivity occur simultaneously in tropical woody forest ecosystems, and root mortality is usually recorded with rhizotron and minirhizotron approaches. Some tropical studies reported that fine root mortality is negatively related to soil cation exchange capacity and soil pH and positively related to soil sand content, which may reflect decreasing soil nutrient content (Silver & Vogt, 1993; Varner, 2003). Mean annual precipitation is related to root mortality (Cordeiro et al., 2020; Green et al., 2005). Data on fine root mortality are limited for tropical forests.

Root residence time is the ratio of root carbon stock and productivity, or how long root biomass remains with the living structures of root tissues, and it is also the inverse of root turnover (Friend et al., 2014; Galbraith et al., 2013; Sierra Cornejo et al., 2020). Root productivity, turnover, and decomposition are the main source of fluxes of C and N in lowland forest soils (Friend et al., 2014; Silver et al., 2005). Root turnover depends both on climatic and soil conditions. Global analysis of root turnover revealed that turnover increased exponentially with mean annual temperature and decreased from tropical regions to temperate regions (Gill & Jackson, 2000; McCormack & Guo, 2014). Root turnover has a positive

relationship with soil P (Okada et al., 2017; Sierra Cornejo et al., 2020), N (Graefe et al., 2008; Ostertag, 2001), and K (Yavitt et al., 2011). Root turnover decreases with soil depth, with longer-lived roots in deeper soil layers (Cordeiro et al., 2020; Joslin et al., 2006).

Fractional carbon allocation of total NPP to the fine root growth varies across pantropical forests and along soil nutrient gradients. Low soil nutrient and water content results in increased carbon allocation to the fine roots, to boost nutrient and water uptake from the soil (Assefa et al., 2017; Cairns et al., 1997; Yavitt et al., 2011). Soils with high sand content have poorer water holding capacity, and root carbon allocation on such soils is higher than on clay soils (Aragão et al., 2009; Silver et al., 2005; Yuan & Chen, 2010). This high allocation of carbon to the fine roots may also reflect the decreased productivity of the aboveground components (Kochsiek et al., 2013; Kramer-Walter & Laughlin, 2017). Early studies of carbon allocation in tropical forests showed that on average 27% of the total primary productivity was allocated to the fine roots (Malhi et al., 2011). In the last decades, more studies of forest ecosystem carbon allocation have been reported with increasing detail. In Amazon forests, fractional carbon allocation to the fine roots range between 16% and 41%, with a highest percentage recorded in Terra Preta forests and the lowest in western Amazon forests (Araujo-Murakami et al., 2014; Doughty et al., 2014; Malhi et al., 2017; Rocha et al., 2014). In western African forests, fractional allocation of 33% (Moore et al., 2018), and in Southeast Asian forests, the lowest fractional allocation that ranges between 10% and 14% (Kho et al., 2013; Riutta et al., 2018) have been reported. Along elevation gradients, fractional carbon allocation of total NPP to fine roots is one of the key determinants of the plant carbon budget, allocation to fine root increasing with elevation, driven by changes in soil nutrient content and climatic variables (Moser et al., 2011; Sierra Cornejo et al., 2020). In Malaysian Bornean montane forests, root carbon allocation increased with decreasing N as a critical element (Okada et al., 2017).

Fine root morphological traits are key features for soil nutrient uptake, and they are vital to compete for soil resources where soil nutrients are scarce (Freschet et al., 2020). For example, plant species occurring on P limited soils in tropical lowland forests show high root length growth and high specific root length (Addo-Danso et al., 2020; Hogan et al., 2020; Lambers et al., 2006), because these are key traits for phosphorus assimilation efficiency (Lugli et al., 2019). Tropical lowland soil fertilization with N, P, and K decreases fine root length and tissue density (Wurzburger & Wright, 2015). In contrast, the scarcity of soil nutrients in sandy soils increases root length and surface area growth as an ecological strategy for soil nutrient uptake (Kochsiek et al., 2013; Silver et al., 2000).

Variation of root morphological dynamics in relation to climatic factors has been poorly studied. Some drought experiments reported that fine root length and surface area growth increase with increasing soil water (Andrade et al., 2020; Rodtassana & Tanner, 2018). On the other hand, a pantropical study reported that mean annual precipitation and temperature had no significant influence on most root morphological traits, but temperature explained a small proportion of specific root length (Addo-Danso et al., 2020).

Some root morphological traits studies have been carried out in tropical montane forests and they reported that soil C:N ratio increases root length growth and specific root length (Graefe et al., 2008; Moser et al., 2010; Sierra Cornejo et al., 2020), however the relationship between C:N and other traits is still unknown. Overall, information on root morphological traits and their relationship with environmental factors in montane forests remain poorly understood.

2.6 References

Adamek, M., Corre, M. D., & Hölscher, D. (2011). Responses of fine roots to experimental nitrogen addition in a tropical lower montane rain forest, Panama. *Journal of Tropical Ecology*, *27*(1), 73–81. https://doi.org/10.1017/S0266467410000507

Addo-Danso, S. D., Defrenne, C. E., Luke, E. D. M., Ostonen, I., Ernest, A. A., Kira, G. F., … Prescott, C. E. (2020). Fine-root morphological trait variation in tropical forest ecosystems : an evidence synthesis. *Plant Ecology*, *221*(1), 1–13. https://doi.org/10.1007/s11258-019-00986-1

Addo-Danso, S. D., Prescott, C. E., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Guy, R. D.,

… Malhi, Y. (2018). Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. *Biotropica*, *50*(4), 606–615. https://doi.org/10.1111/btp.12556

Addo-Danso, S. D., Prescott, C. E., & Smith, A. R. (2016). Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. *Forest Ecology and Management*, *359*, 332–351. https://doi.org/10.1016/j.foreco.2015.08.015

Adhikari, H., Valbuena, R., Pellikka, P. K. E., & Heiskanen, J. (2020). Mapping forest structural heterogeneity of tropical montane forest remnants from airborne laser scanning and Landsat time series. *Ecological Indicators*, *108*, 105739. https://doi.org/10.1016/j.ecolind.2019.105739

Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F., & Poorter, L. (2019). Amazonian rainforest tree mortality driven by climate and functional traits. *Nature Climate Change*, *9*(5), 384–388. https://doi.org/10.1038/s41558-019-0458-0

Aleman, J. C., Jarzyna, M. A., & Staver, A. C. (2018). Forest extent and deforestation in tropical Africa since 1900. *Nature Ecology & Evolution*, *2*(1), 26–33. https://doi.org/10.1038/s41559-017-0406-1

Allen, K., Fisher, J. B., Phillips, R. P., Powers, J. S., & Brzostek, E. R. (2020). Modeling the Carbon Cost of Plant Nitrogen and Phosphorus Uptake Across Temperate and Tropical Forests. *Frontiers in Forests and Global Change*, *3*(May), 1–12. https://doi.org/10.3389/ffgc.2020.00043

Andrade, E. M. De, Rosa, G. Q., Almeida, A. M. M. De, Silva, A. G. R. Da, & Sena, M. G. T. (2020). Rainfall regime on fine root growth in a seasonally dry tropical forest. *Revista Caatinga*, *33*(2), 458–469. https://doi.org/10.1590/1983-21252020v33n218rc

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Araujo-Murakami, A., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., … Malhi, Y. (2014). The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecology & Diversity*, *7*(1–2), 55–69. https://doi.org/10.1080/17550874.2013.798364

Assefa, D., Rewald, B., Sandén, H., & Godbold, D. L. (2017). Fine Root Dynamics in Afromontane Forest and Adjacent Land Uses in the Northwest Ethiopian Highlands. *Forests*, *8*(7), 249. https://doi.org/10.3390/f8070249

Baker, T. R., Burslem, D. F. R. P., & Swaine, M. D. (2003). Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. *Journal of Tropical Ecology*, *19*(2), 109–125. https://doi.org/10.1017/S0266467403003146

Banda, K. R., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., … Pennington, R. T. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science*, *353*(6306). https://doi.org/10.1126/science.aaf5080

Bendix, J., Beck, E., Bräuning, A., Makeschin, F., & Mosandl, R. (2013). *Ecosystem Services , Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador*.

Blonder, B., Salinas, N., Patrick Bentley, L., Shenkin, A., Chambi Porroa, P. O., Valdez Tejeira, Y., … Malhi, Y. (2017). Predicting trait-environment relationships for venation networks along an Andes-Amazon elevation gradient. *Ecology*, *98*(5), 1239–1255. https://doi.org/10.1002/ecy.1747

Bodart, C., Brink, A. B., Donnay, F., Lupi, A., Mayaux, P., & Achard, F. (2013). Continental estimates of forest cover and forest cover changes in the dry ecosystems of Africa between 1990 and 2000. *Journal of Biogeography*, *40*(6), 1036–1047. https://doi.org/10.1111/jbi.12084

Brando, P. M., Paolucci, L., Ummenhofer, C. C., Ordway, E. M., Hartmann, H., Cattau, M., … Balch, J. (2019). Droughts, Wildfires, and Forest Carbon Cycling : A Pantropical Synthesis. *Annual Reviews*, 555–581. https://doi.org/10.1146/annurev-earth-082517-010235

Brienen, R. J. W., Phillips, O. L., Feldpausch, T. R., Gloor, E., Baker, T. R., Lloyd, J., … Zagt, R. J. (2015). Long-term decline of the Amazon carbon sink. *Nature*, *519*(7543), 344–348. https://doi.org/10.1038/nature14283

Bruijnzeel, L. A., Kappelle, M., Mulligan, M., & Scatena, F. N. (2011). Tropical montane cloud forests: State of knowledge and sustainability perspectives in a changing world. Tropical Montane Cloud Forests*: Science for Conservation and Management*. https://doi.org/10.1017/CBO9780511778384.074

Bubb, P., May, I., Miles, L., & Sayer, J. (2004). Cloud Forest Agenda.

Cairns, M. A., Brown, S., Helmer, E. H., & Baumgardner, G. a. (1997). Root biomass allocation in the world's upland forests. *Oecologia*, *111*(1), 1–11. https://doi.org/10.1007/s004420050201

Campos C., A., Cruz H., L., & Rocha O., S. (2017). Mass, nutrient pool, and mineralization of litter and fine roots in a tropical mountain cloud forest. *Science of The Total Environment*, *575*, 876–886. https://doi.org/10.1016/j.scitotenv.2016.09.126

Castanho, A. D. A., Coe, M. T., Costa, M. H., Malhi, Y., Galbraith, D., & Quesada, C. A. (2013). Improving simulated Amazon forest biomass and productivity by including spatial variation in biophysical parameters. *Biogeosciences*, *10*(4), 2255–2272. https://doi.org/10.5194/bg-10-2255-2013

Cavelier, J., Wright, S. J., & Santamaria, J. (1999). Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. *Plant and Soil*, *211*(2), 207–213. https://doi.org/10.1023/A:1004686204235

Cavelier, Jaime. (1992). Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama. *Plant and Soil*, *142*(2), 187–201. https://doi.org/10.1007/BF00010965

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde-Barrantes, O., Fuchslueger, L., Oblitas, E., … Quesada, C. A. (2020). Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant-Environment Interactions*, *1*(1), 3–16. https://doi.org/10.1002/pei3.10010

Cusack, D. F., Markesteijn, L., Condit, R., Lewis, O. T., & Turner, B. L. (2018). Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots. *Biogeochemistry*, *137*(1–2), 253–266. https://doi.org/10.1007/s10533-017-0416-8

Deans, J. D., Moran, J., & Grace, J. (1996). Biomass relationships for tree species in regenerating semi-deciduous tropical moist forest in Cameroon. *Forest Ecology and Management*, *88*(3), 215–225. https://doi.org/10.1016/S0378-1127(96)03843-1

del Aguila-Pasquel, J., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Girardin, C. A. J., Chung Gutierrez, J. A., … Malhi, Y. (2014). The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology & Diversity*, *7*(1–2), 71–83. https://doi.org/10.1080/17550874.2013.798365

Doughty, C. E., Metcalfe, D. B., da Costa, M. C. L., de Oliveira, A. A. R., Neto, G. F. C., Silva, J. A., … Malhi, Y. (2014). The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile

soil. *Plant Ecology & Diversity*, *7*(1–2), 41–53. https://doi.org/10.1080/17550874.2013.798367

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huaraca Huasco, W., … Malhi, Y. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541), 78–82. https://doi.org/10.1038/nature14213

Drewniak, B. A. (2019). Simulating Dynamic Roots in the Energy Exascale Earth System Land Model. *Journal of Advances in Modeling Earth Systems*, *11*(1), 338–359. https://doi.org/10.1029/2018MS001334

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlstrom, A., Lissa, C. J. van, Zhao, X., … Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, *195*, 260–262. https://www.nature.com/articles/s41561-019-0530-4

Espeleta, J. F., & Clark, D. A. (2007). Multi-scale variation in fine-root biomass in a tropical rain forest: a seven-year study. *Ecological Monographs*, *77*(3), 377–404. https://doi.org/10.1890/06-1257.1

Eva, H. D., Belward, A. S., De Miranda, E. E., Di Bella, C. M., Gond, V., Huber, O., … Fritz, S. (2004). A land cover map of South America. *Global Change Biology*, *10*(5), 731–744. https://doi.org/10.1111/j.1529-8817.2003.00774.x

Feng, X., Porporato, A., & Rodriguez-Iturbe, I. (2013). Changes in rainfall seasonality in the tropics. *Nature Climate Change*, *3*(9), 811–815. https://doi.org/10.1038/nclimate1907

Freschet, G., Pagès, L., Iversen, C., Comas, L., Rewald, B., Roumet, C., … Postma, J. (2020). A starting guide to root ecology: Strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements, (August).

Freycon, V., Wonkam, C., Fayolle, A., Laclau, J. P., Lucot, E., Jourdan, C., … Gourlet-Fleury, S. (2015). Tree roots can penetrate deeply in African semi-deciduous rain forests: Evidence from two common soil types. *Journal of Tropical Ecology*, *31*(1), 13–23. https://doi.org/10.1017/S0266467414000595

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., … Woodward, F. I. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. *Proceedings of the National Academy of Sciences*, *111*(9), 3280–3285. https://doi.org/10.1073/pnas.1222477110

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D. A., Doughty, C. E., Fisher, R. A., … Lloyd, J. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, *6*(1), 139–157. https://doi.org/10.1080/17550874.2013.770578

Gathorne-Hardy, F. J., Syaukani, Davies, R. G., Eggleton, P., & Jones, D. T. (2002). Quaternary rainforest refugia in south-east Asia: using termites (Isoptera) as indicators. *Biological Journal of the Linnean Society*, *75*(4), 453–466. https://doi.org/10.1046/j.1095-8312.2002.00031.x

Gatti, L. V., Gloor, M., Miller, J. B., Doughty, C. E., Malhi, Y., Domingues, L. G., … Lloyd, J. (2014). Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature*, *506*(7486), 76–80. https://doi.org/10.1038/nature12957

Gaveau, D. L. A., Locatelli, B., Salim, M. A., Yaen, H., Pacheco, P., & Sheil, D. (2019). Rise and fall of forest loss and industrial plantations in Borneo (2000-2017). *Conservation Letters*, *12*(3), e12622. https://doi.org/10.1111/conl.12622

Germon, A., Laclau, J.-P., Robin, A., & Jourdan, C. (2020). Tamm Review: Deep fine roots in forest ecosystems: Why dig deeper? *Forest Ecology and Management*, *466*, 118135. https://doi.org/10.1016/j.foreco.2020.118135

Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, *147*(1), 13–31. https://doi.org/10.1046/j.1469-8137.2000.00681.x

Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient

in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082

Girardin, Cécile A.J., Espejo, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., … Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

Goldstein, G. (2016). *Tropical Tree Physiology*. (G. Goldstein & L. S. Santiago, Eds.) (Vol. 6). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-27422-5

Graefe, S., Hertel, D., & Leuschner, C. (2008). Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil*, *313*(1–2), 155–166. https://doi.org/10.1007/s11104-008-9688-z

Green, J. J., Dawson, L. A., Proctor, J., Duff, E. I., & Elston, D. A. (2005). Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. *Plant and Soil*, *276*(1–2), 23–32. https://doi.org/10.1007/s11104-004-0331-3

Hasnat, G. N. T., & Hossain, M. K. (2020). Global Overview of Tropical Dry Forests. In *Handbook of Research on the Conservation and Restoration of Tropical Dry Forests* (pp. 1–23). https://doi.org/10.4018/978-1-7998-0014-9.ch001

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., & Leuschner, C. (2009). Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. *Forest Ecology and Management*, *258*(9), 1904–1912. https://doi.org/10.1016/j.foreco.2009.07.019

Hogan, J. A., Valverde-Barrantes, O. J., Ding, Q., Xu, H., & Baraloto, C. (2020). Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China. *Annals of Forest Science*, *77*(3), 79. https://doi.org/10.1007/s13595-020-00977-7

Hölscher, D., Dunker, B., Harbusch, M., & Corre, M. (2009). Fine Root Distribution in a Lower Montane Rain Forest of Panama. *Biotropica*, *41*(3), 312–318. https://doi.org/10.1111/j.1744-7429.2009.00492.x

Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Ibrahim, F., Adu-Bredu, S., Addo-Danso, S. D., Duah-Gyamfi, A., Manu, E. A., & Malhi, Y. (2020). Patterns and controls on fine-root dynamics along a rainfall gradient in Ghana. *Trees*, 1–13. https://doi.org/10.1007/s00468-020-01970-3

Ibrahima, A., Mvondo ZE, A., & Ntonga, J. (2010). Fine root production and distribution in the tropical rainforests of south-western Cameroon: effects of soil type and selective logging. *IForest - Biogeosciences and Forestry*, *3*(5), 130–136. https://doi.org/10.3832/ifor0549-003

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., … Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26. https://doi.org/10.1111/nph.14486

Jackson, R. B., Mooney, H. A., & Schulze, E. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(14), 7362–7366. https://doi.org/10.1073/pnas.94.14.7362

Jiménez, E M, Moreno, F. H., Lloyd, J., Peñuela, M. C., & Patiño, S. (2009). Fine root dynamics for forests on contrasting soils in the colombian Amazon. *Biogeosciences Discussions*, *6*(2), 3415–3453. https://doi.org/10.5194/bgd-6-3415-2009

Jiménez, Eliana M., Peñuela-Mora, M. C., Moreno, F., & Sierra, C. A. (2020). Spatial and temporal variation of forest net primary productivity components on contrasting soils in northwestern Amazon. *Ecosphere*, *11*(8). https://doi.org/10.1002/ecs2.3233

Joslin, J. D., Gaudinski, J. B., Torn, M. S., Riley, W. J., & Hanson, P. J. (2006). Fine-root turnover patterns and their relationship to root diameter and soil depth in a 14C-labeled hardwood forest. *New Phytologist*, *172*(3), 523–535. https://doi.org/10.1111/j.1469-8137.2006.01847.x

Jucker, T., Asner, G. P., Dalponte, M., Brodrick, P., Christopher, D., Vaughn, N., … Reynolds, G. (2018). Estimating aboveground carbon density and its uncertainty in Borneo ' s structurally complex tropical forests using airborne laser scanning. *Biogeosciences*, (March), 1–29.

Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A., & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO Global Forest Resources Assessment 2015. *Forest Ecology and Management*, *352*, 9–20. https://doi.org/10.1016/j.foreco.2015.06.014

Kettle, C. J. (2010). Ecological considerations for using dipterocarps for restoration of lowland rainforest in Southeast Asia. *Biodiversity and Conservation*, *19*(4), 1137–1151. https://doi.org/10.1007/s10531-009-9772-6

Kho, L. K., Malhi, Y., & Tan, S. K. S. (2013). Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo. *Journal of Geophysical Research: Biogeosciences*, *118*(3), 1282–1296. https://doi.org/10.1002/jgrg.20109

Kochsiek, A., Tan, S., & Russo, S. E. (2013). Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology*, *214*(6), 869–882. https://doi.org/10.1007/s11258-013-0215-9

Kooyman, R. M., Morley, R. J., Crayn, D. M., Joyce, E. M., Rossetto, M., Slik, J. W. F., … Wilf, P. (2019). Origins and Assembly of Malesian Rainforests. *Annual Review of Ecology, Evolution, and Systematics*, *50*(1), 119–143. https://doi.org/10.1146/annurev-ecolsys-110218-024737

Kramer-Walter, K. R., & Laughlin, D. C. (2017). Root nutrient concentration and biomass allocation are more plastic than morphological traits in response to nutrient limitation. *Plant and Soil*, *416*(1–2), 539–550. https://doi.org/10.1007/s11104-017-3234-9

Laliberté, E. (2017). Below-ground frontiers in trait-based plant ecology. *New Phytologist*, *213*(4), 1597–1603. https://doi.org/10.1111/nph.14247

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J., & Veneklaas, E. J. (2006). Root Structure and Functioning for Efficient Acquisition of Phosphorus: Matching Morphological and Physiological Traits. *Annals of Botany*, *98*(4), 693–713. https://doi.org/10.1093/aob/mcl114

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M., & Hertel, D. (2007). Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology*, *8*(3), 219–230. https://doi.org/10.1016/j.baae.2006.02.004

Leuschner, C., Wiens, M., Harteveld, M., Hertel, D., & Tjitrosemito, S. (2006). Patterns of Fine Root Mass and Distribution along a Disturbance Gradient in a Tropical Montane Forest, Central Sulawesi (Indonesia). *Plant and Soil*, *283*(1–2), 163–174. https://doi.org/10.1007/s11104-006-6638-5

Lugli, L. F., Andersen, K. M., Aragão, L. E. O. C., Cordeiro, A. L., Cunha, H. F. V., Fuchslueger, L., … Hartley, I. P. (2019). Multiple phosphorus acquisition strategies

adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil*, *450*(1–2), 49–63. https://doi.org/10.1007/s11104-019-03963-9

Malhi, Y. (2018). Ancient deforestation in the green heart of Africa. *Proceedings of the National Academy of Sciences*, *115*(13), 3202–3204. https://doi.org/10.1073/pnas.1802172115

Malhi, Y., Adu-bredu, S., Asare, R. A., Lewis, S. L., & Mayaux, P. (2013). African rainforests : past , present and future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1625), 20120312. Retrieved from https://doi.org/10.1098/rstb.2012.0312

Malhi, Y., del Aguilla-Pasquell, J., Metcalfe, D. B., Phillips, O. L., Farfan-Rios, W., Silman, M., … Farfán Amézquita, F. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., … Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, *21*(6), 2283–2295. https://doi.org/10.1111/gcb.12859

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1582), 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Farfán Amézquita, F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., … Phillips, O. L. (2014a). The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology and Diversity*, *7*(1–2), 85–105. https://doi.org/10.1080/17550874.2013.820805

Malhi, Y., Farfán Amézquita, F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., … Phillips, O. L. (2014b). The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology & Diversity*, *7*(1–2), 85–105. https://doi.org/10.1080/17550874.2013.820805

Malhi, Y., & Grace, J. (2000). Tropical forests and atmospheric carbon dioxide. *Trends in Ecology & Evolution*, *15*(8), 332–337. https://doi.org/10.1016/S0169-5347(00)01906-6

Marimon, B. S., Marimon-Junior, B. H., Feldpausch, T. R., Oliveira-Santos, C., Mews, H. A., Lopez-Gonzalez, G., … Phillips, O. L. (2014). Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. *Plant Ecology & Diversity*, *7*(1–2), 281–292. https://doi.org/10.1080/17550874.2013.818072

Marthews, T. R., Malhi, Y., Girardin, C. A. J., Silva Espejo, J. E., Aragão, L. E. O. C., Metcalfe, D. B., … Williams, R. J. (2012). Simulating forest productivity along a neotropical elevational transect: temperature variation and carbon use efficiency. *Global Change Biology*, *18*(9), 2882–2898. https://doi.org/10.1111/j.1365-2486.2012.02728.x

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., … Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *The New Phytologist*, *207*(3), 505–518. https://doi.org/10.1111/nph.13363

McCormack, M. L., & Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science*, *5*, 205. https://doi.org/10.3389/fpls.2014.00205

McCormack, M. L., Guo, D., Iversen, C. M., Chen, W., Eissenstat, D. M., Fernandez, C. W., … Zanne, A. (2017). Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist*, *215*(1), 27–37. https://doi.org/10.1111/nph.14459

McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., … Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world.

Science, *368*(6494). https://doi.org/10.1126/science.aaz9463

Metcalfe, D. B., Meir, P., Aragão, L. E. O. C., da Costa, A. C. L., Braga, A. P., Gonçalves, P. H. L., … Williams, M. (2008). The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, *311*(1–2), 189–199. https://doi.org/10.1007/s11104-008-9670-9

Miles, L., Newton, A. C., DeFries, R. S., Ravilious, C., May, I., Blyth, S., … Gordon, J. E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, *33*(3), 491–505. https://doi.org/10.1111/j.1365-2699.2005.01424.x

Moonlight, P. W., Banda-R, K., Phillips, O. L., Dexter, K. G., Pennington, R. T., Baker, T. R., … Veenendaal, E. (2020). Expanding tropical forest monitoring into Dry Forests: The DRYFLOR protocol for permanent plots. *Plants, People, Planet*, 1–6. https://doi.org/10.1002/ppp3.10112

Moore, S., Adu-Bredu, S., Duah-Gyamfi, A., Addo-Danso, S. D., Ibrahim, F., Mbou, A. T., … Malhi, Y. (2018). Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. *Global Change Biology*, *24*(2), e496–e510. https://doi.org/10.1111/gcb.13907

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., & Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*, *17*(6), 2211–2226. https://doi.org/10.1111/j.1365-2486.2010.02367.x

Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., & Hertel, D. (2010). Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity*, *3*(2), 151–164. https://doi.org/10.1080/17550874.2010.517788

Okada, K., Aiba, S., & Kitayama, K. (2017). Influence of temperature and soil nitrogen and phosphorus availabilities on fine-root productivity in tropical rainforests on Mount Kinabalu, Borneo. *Ecological Research*, *32*(2), 145–156. https://doi.org/10.1007/s11284-016-1425-0

Ostertag, R. (2001). Effect of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology*, *82*(2), 485–499. https://doi.org/10.1890/0012-9658(2001)082[0485:EONAPA]2.0.CO;2

Ouedraogo, I., Savadogo, P., Tigabu, M., Cole, R., Oden, P. C., & Ouadba, J. M. (2011). Trajectory analysis of forest cover change in the tropical dry forest of Burkina Faso, West Africa. *Landscape Research*, *36*(3), 303–320. https://doi.org/10.1080/01426397.2011.564861

Pappoe, A. N. M., Armah, F. A., Quaye, E. C., Kwakye, P. K., & Buxton, G. N. T. (2010). Composition and stand structure of a tropical moist semi-deciduous forest in Ghana. *International Research Journal of Plant Science*, *1*(4), 095–106. http://www.interesjournals.org/IRJPS

Pearson, T. R. H., Brown, S., Murray, L., & Sidman, G. (2017). Greenhouse gas emissions from tropical forest degradation: an underestimated source. *Carbon Balance and Management*, *12*(1), 3. https://doi.org/10.1186/s13021-017-0072-2

Peng, Y., Guo, D., & Yang, Y. (2017). Global patterns of root dynamics under nitrogen enrichment. *Global Ecology and Biogeography*, *26*(1), 102–114. https://doi.org/10.1111/geb.12508

Pennington, R. T., Lehmann, C. E. R., & Lucy M. Rowland. (2018). Tropical savannas and dry forests. *Current Biology*, *28*, 527–548. https://doi.org/10.1016/j.cub.2018.03.014

Piñeiro, R., Dauby, G., Kaymak, E., & Hardy, O. J. (2017). Pleistocene population expansions of shade-tolerant trees indicate fragmentation of the African rainforest during the Ice Ages. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1866), 20171800.

https://doi.org/10.1098/rspb.2017.1800
Portillo-Quintero, C. A., & Sánchez-Azofeifa, G. A. (2010). Extent and conservation of tropical dry forests in the Americas. *Biological Conservation*, *143*(1), 144–155. https://doi.org/10.1016/j.biocon.2009.09.020
Potapov, P., Hansen, M. C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., … Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances*, *3*(1), e1600821. https://doi.org/10.1126/sciadv.1600821
Powers, J. S., Becklund, K. K., Gei, M. G., Iyengar, S. B., Meyer, R., O'Connell, C. S., … Werden, L. K. (2015). Nutrient addition effects on tropical dry forests: A mini-review from microbial to ecosystem scales. *Frontiers in Earth Science*, *3*(June), 1–8. https://doi.org/10.3389/feart.2015.00034
Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J. (2014). Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences*, *111*(38), 13721–13726. https://doi.org/10.1073/pnas.1216053111
Rifai, S. W., Girardin, C. A. J., Berenguer, E., del Aguila-Pasquel, J., Dahlsjö, C. A. L., Doughty, C. E., … Malhi, Y. (2018). ENSO Drives interannual variation of forest woody growth across the tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1760), 20170410. https://doi.org/10.1098/rstb.2017.0410
Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M., … Ewers, R. M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology*, *24*(7), 2913–2928. https://doi.org/10.1111/gcb.14068
Rocha, W., Metcalfe, D. B., Doughty, C. E., Brando, P., Silvério, D., Halladay, K., … Malhi, Y. (2014). Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). *Plant Ecology & Diversity*, *7*(1–2), 25–40. https://doi.org/10.1080/17550874.2013.798368
Röderstein, M., Hertel, D., & Leuschner, C. (2005). Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, *21*(5), 483–492. https://doi.org/10.1017/S026646740500249X
Rodtassana, C., & Tanner, E. V. J. (2018). Litter removal in a tropical rain forest reduces fine root biomass and production but litter addition has few effects. *Ecology*, *99*(3), 735–742. https://doi.org/10.1002/ecy.2143
Sánchez-Azofeifa, G. A., Quesada, M., Rodríguez, J. P., Nassar, J. M., Stoner, K. E., Castillo, A., … Cuevas-Reyes, P. (2005). Research priorities for neotropical dry forests. *Biotropica*, *37*(4), 477–485. https://doi.org/10.1111/j.1744-7429.2005.00066.x
Sánchez-Gallén, I., & Alvarez-Sánchez, J. (1996). Root productivity in a lowland tropical rain forest in Mexico. *Vegetatio*, *123*(2), 109–115. https://doi.org/10.1007/BF00118265
Sayre, R., Karagulle, D., Frye, C., Boucher, T., Wolff, N. H., Breyer, S., … Possingham, H. (2020). An assessment of the representation of ecosystems in global protected areas using new maps of World Climate Regions and World Ecosystems. *Global Ecology and Conservation*, *21*, e00860. https://doi.org/10.1016/j.gecco.2019.e00860
Scatena, F. N., Bruijnzeel, L. A., Bubb, P., & Das, S. (2010). Setting the Stage. In *Tropical Montane Cloud Forests* (pp. 3–13).
Sierra Cornejo, N., Hertel, D., Becker, J. N., Hemp, A., & Leuschner, C. (2020). Biomass, Morphology, and Dynamics of the Fine Root System Across a 3,000-M Elevation Gradient on Mt. Kilimanjaro. *Frontiers in Plant Science*, *11*, 13. https://doi.org/10.3389/fpls.2020.00013
Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., & Cosme, R. (2000). Effects

of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. *Ecosystems*, *3*(2), 193–209. https://doi.org/10.1007/s100210000019

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., … Keller, M. (2005). Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology*, *11*(2), 290–306. https://doi.org/10.1111/j.1365-2486.2005.00903.x

Silver, W. L., & Vogt, K. A. (1993). Fine Root Dynamics Following Single and Multiple Disturbances in a Subtropical Wet Forest Ecosystem. *The Journal of Ecology*, *81*(4), 729. https://doi.org/10.2307/2261670

Sodhi, N. S., Posa, M. R. C., Lee, T. M., Bickford, D., Koh, L. P., & Brook, B. W. (2010). The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation*, *19*(2), 317–328. https://doi.org/10.1007/s10531-009-9607-5

Soethe, N., Lehmann, J., & Engels, C. (2006). The Vertical Pattern of Rooting and Nutrient Uptake at Different Altitudes of a South Ecuadorian Montane Forest. *Plant and Soil*, *286*(1–2), 287–299. https://doi.org/10.1007/s11104-006-9044-0

Soh, M. C. K., Mitchell, N. J., Ridley, A. R., Butler, C. W., Puan, C. L., & Peh, K. S.-H. (2019). Impacts of Habitat Degradation on Tropical Montane Biodiversity and Ecosystem Services: A Systematic Map for Identifying Future Research Priorities. *Frontiers in Forests and Global Change*, *2*, 1–18. https://doi.org/10.3389/ffgc.2019.00083

Spracklen, D. V., & Righelato, R. (2014). Tropical montane forests are a larger than expected global carbon store. *Biogeosciences*, *11*(10), 2741–2754. https://doi.org/10.5194/bg-11-2741-2014

Sullivan, M. J. P., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., … Phillips, O. L. (2020). Long-term thermal sensitivity of Earth's tropical forests. *Science*, *368*(800), 869–874. http://doi.org/10.1126/science.aaw7578

Sullivan, M. J. P., Talbot, J., Lewis, S. L., Phillips, O. L., Qie, L., Begne, S. K., … Zemagho, L. (2017). Diversity and carbon storage across the tropical forest biome. *Scientific Reports*, *7*(1), 39102. https://doi.org/10.1038/srep39102

Tanner, E. V. J., Vitousek, P. M., & Cuevas, E. (1998). Experimental investigation of nutrient limitation of forests growth on wet tropical mountains. *Ecology*, *79*(1), 10–22.

Telles, E. de C. C., de Camargo, P. B., Martinelli, L. A., Trumbore, S. E., da Costa, E. S., Santos, J., … Oliveira, R. C. (2003). Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles*, *17*(2). https://doi.org/10.1029/2002GB001953

Ter Steege, H., Mota de Oliveira, S., Pitman, N. C. A., Sabatier, D., Antonelli, A., Guevara Andino, J. E., … Salomão, R. P. (2019). Towards a dynamic list of Amazonian tree species. *Scientific Reports*, *9*(1), 3501. https://doi.org/10.1038/s41598-019-40101-y

Tuomisto, H., Van doninck, J., Ruokolainen, K., Moulatlet, G. M., Figueiredo, F. O. G., Sirén, A., … Zuquim, G. (2019). Discovering floristic and geoecological gradients across Amazonia. *Journal of Biogeography*, *46*(8), 1734–1748. https://doi.org/10.1111/jbi.13627

Uning, R., Latif, M. T., Othman, M., Juneng, L., Mohd Hanif, N., Nadzir, M. S. M., … Takriff, M. S. (2020). A Review of Southeast Asian Oil Palm and Its CO2 Fluxes. *Sustainability*, *12*(12), 5077. https://doi.org/10.3390/su12125077

Valverde-Barrantes, O. J., Raich, J. W., & Russell, A. E. (2007). Fine-root mass, growth and nitrogen content for six tropical tree species. *Plant and Soil*, *290*(1–2), 357–370. https://doi.org/10.1007/s11104-006-9168-2

Van Bloem, S. J., Murphy, P. G., & Lugo, A. E. (2004). TROPICAL FORESTS | Tropical Dry Forests. In *Encyclopedia of Forest Sciences* (pp. 1767–1775). https://doi.org/10.1016/B0-

12-145160-7/00176-9

Varner, R. K. (2003). Experimentally induced root mortality increased nitrous oxide emission from tropical forest soils. *Geophysical Research Letters*, *30*(3), 1144. https://doi.org/10.1029/2002GL016164

Vourlitis, G. L., De Souza Nogueira, J., De Almeida Lobo, F., Sendall, K. M., De Paulo, S. R., Antunes Dias, C. A., … De Andrade, N. L. R. (2008). Energy balance and canopy conductance of a tropical semi-deciduous forest of the southern Amazon Basin. *Water Resources Research*, *44*(3), 1–14. https://doi.org/10.1029/2006WR005526

Wade, A. M., Richter, D. D., Medjibe, V. P., Bacon, A. R., Heine, P. R., White, L. J. T., & Poulsen, J. R. (2019). Estimates and determinants of stocks of deep soil carbon in Gabon, Central Africa. *Geoderma*, *341*, 236–248. https://doi.org/10.1016/j.geoderma.2019.01.004

Wang, C., Chen, Z., Brunner, I., Zhang, Z., Zhu, X., Li, J., … Li, M.-H. (2018). Global patterns of dead fine root stocks in forest ecosystems. *Journal of Biogeography*, *45*(6), 1378–1394. https://doi.org/10.1111/jbi.13206

Wigneron, J.-P., Fan, L., Ciais, P., Bastos, A., Brandt, M., Chave, J., … Fensholt, R. (2020). Tropical forests did not recover from the strong 2015-2016 El Niño event. *Science Advances*, *6*(6), eaay4603. https://doi.org/10.1126/sciadv.aay4603

Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., … Corre, M. D. (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, *92*(8), 1616–1625. https://doi.org/10.1890/10-1558.1

Wurzburger, N., & Wright, S. J. (2015). Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology*, *96*(8), 2137–2146. https://doi.org/10.1890/14-1362.1

Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., & Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecology*, *36*(4), 433–445. https://doi.org/10.1111/j.1442-9993.2010.02157.x

Yuan, Z. Y., & Chen, H. Y. H. (2010). Fine Root Biomass, Production, Turnover Rates, and Nutrient Contents in Boreal Forest Ecosystems in Relation to Species, Climate, Fertility, and Stand Age: Literature Review and Meta-Analyses. *Critical Reviews in Plant Sciences*, *29*(4), 204–221. https://doi.org/10.1080/07352689.2010.483579

Yuan, Z. Y., & Chen, H. Y. H. (2012). A global analysis of fine root production as affected by soil nitrogen and phosphorus. *Proceedings. Biological Sciences*, *279*(1743), 3796–3802. https://doi.org/10.1098/rspb.2012.0955

Yuan, Z. Y., Chen, H. Y. H., & Reich, P. B. (2011). Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nature Communications*, *2*(1), 344. https://doi.org/10.1038/ncomms1346

Zhu, F., Yoh, M., Gilliam, F. S., Lu, X., & Mo, J. (2013). Nutrient Limitation in Three Lowland Tropical Forests in Southern China Receiving High Nitrogen Deposition: Insights from Fine Root Responses to Nutrient Additions. *PLoS ONE*, *8*(12), e82661. https://doi.org/10.1371

Chapter 3: Site description and methods



Trocha Union transect and Pantiacolla overviews of lowland Amazon in Kosñipata Valley of Peruvian Andes (top right and left panels). Ankasa National Park in Ghana (bottom left corner, photo by Yadvinder Malhi). Danum Valley Conservation Area in Malaysia (bottom right corner)

3.1 Site characteristics

The fine root dynamics and morphological traits studies were carried out in neotropical and paleotropical rainforest ecosystems that span different forest types from lowland to montane forests and from dry to wet forests, encompassing environmental gradients such as elevation, temperature, rainfall and soil fertility. The study examining global patterns in tropical forest fine root dynamics (Chapter 4) was carried out in 47 plots in South America, Africa and Southeast Asia. The study examining vertical and temporal variation in fine root dynamics (Chapter 5) was carried out in 19 plots in Amazon forests of Bolivia, Brazil, and Peru. The study examining fine root morphological traits (Chapter 6) was carried out in 15 plots in Amazon and Andean forests of Peru. All study sites were part of the Global Ecosystem Monitoring (GEM) network. GEM is a network in tropical and temperate sites where productivity and carbon allocation of forest ecosystems, and their plant functional traits, soil, and climate, has been monitored using standard protocols since 2005 (Malhi et al., 2021, http://gem.tropicalforests.ox.ac.uk/, http://gem.tropicalforests.ox.ac.uk/page/resources).

3.1.1 South America

3.1.1.1 Bolivia: two lowland plots

In Bolivia, between moist Amazon and Chiquitano deciduous forests, two one-hectare plots were set up in 2008, on private property at the hacienda Kenia (KEN) in Guarayos Province, Santa Cruz department. The two semi-deciduous plots are two kilometres apart and are situated on cambisols soil type with high cation exchange capacity and phosphorus concentration (Chapter 4, Table 4.1). The first plot (KEN-01) is located on deeper soil in a slight topographic depression, and the second plot (KEN-02) is located on shallow soil with a less one-meter soil depth, over Precambrian bedrock (Araujo-Murakami et al., 2014; Doughty et al., 2015). The two KEN plots are highly seasonal forests with strongly pronounced seasons in rainfall (Rifai et al., 2018). The rainy season occurs between December and February with rainfall over 200

mm mo^{-1}, and the dry season between April and September with rainfall less than 100 mm mo^{-1}. There is also seasonality in air temperature, with coldest temperature between May and July and mean annual temperature over 24 ºC. The dominant tree species of this ecotone forests between wet Amazon and Chiquitano dry forests are *Ceiba pentandra, Hura crepitans, Pesudolmedia laevis, Schizolobium amazonicum, Swietenia macrophylla, Anadenanthera macrophylla, Caesalpinia pluviosa, Piptadenia viridiflora, and Swetia fruticose* (Araujo-Murakami et al., 2014; Malhi et al., 2015).

3.1.1.2 Brazil: six lowland plots

In Brazilian Amazon regions the GEM plots are located in the states of Mato Grosso and Pará. In the state of Mato Grosso, two deciduous forests are located in Nova Xavantina (NXV) and two in semi-deciduous forests are located in Fazenda Tanguro (TAN). The two NXV deciduous forest plots are situated in the Bacaba Municipality Park. The deciduous forests are on ferrasols soil type with high soil sand content and with low cation exchange capacity (Chapter 4, Table 4.1). These forests exhibit strong seasonal patterns of rainfall and two well-defined seasons, with rainy season between October and March and dry season between April and September. The mean annual temperature is over 25 ºC (de Farias et al., 2016; Neyret et al., 2016). The forest structure and composition of these two forests differ, the first forest (NXV-01) is a savanna woodland and the second forest a tall closed woodland (NXV-02), and they are located in transitional forests and short savanna (Gvozdevaite et al., 2018; Marimon et al., 2014). Gvozdevaite et al. (2018) listed sixty-five tree species for Nova Xavantina forests.

The two semi-deciduous TAN forests are located at 30 km north of southern boundary of the Amazon rainforest. The forests are located on red-yellow ferrasols soil type, with intense dry season between May and September and rainy season between October and March. The forest structure is old growth closed canopy, with 97 species of trees and lianas (Doughty et al., 2015).

Two lowland wet forests are located in the Caxiunã National Forest Reserve (CAX) in the eastern Amazonia. Both study plots are located on highly weathered Acrisols soil type. There is strong seasonality with dry months between July and November with monthly rainfall below 100 m mo^{-1} and the rainy months between December and June (da Costa et al., 2014; Sotta et al., 2006), The forests are tall, with a canopy height that reaches over 35 m and the site elevation is 15 m above river level in dry season (Doughty et al., 2014, 2015).

3.1.1.3 Peru: seven lowland plots and twelve plots along an elevational gradient

Across the Peruvian Amazon and Andean forests, the GEM plots are located in Loreto, Madre de Dios, and Cusco regions. Two lowland forests are located in two old-growth forests of the Research Institute of Peruvian Amazon (IIAP) in Jenaro Herrera (JEN) district and Requena Province. Two lowland wet forests are located in Allpahuayo-Mishana National Reserve (ALP) in the Maynas Province and other three lowland wet forests are located in Tambopata National Reserve (TAM) of Madre de Dios region.

The first two lowland wet forests located in JEN are situated over 125 m asl and the first plot (JEN-01) is situated in Acrisols and second plot (JEN-02) in Podzols soil types. The rainy months range between October and April, and the dry season between May and September (Honorio et al., 2008; Waddell & Crampton, 2020).

The two lowland ALP wet forests are located in haplic gleysol (ALP-11) and haplic arenosol (ALP-12) soil types (Chapter 4, Table 4.1). There is no distinct dry season because the monthly rainfall exceeds 100 mm mo^{-1} and in the rainy season reaches over 300 mm mo^{-1} (Girardin et al., 2014; Girardin et al., 2016). The total number of tree species range between 184 (ALP-11) and 99 (ALP-12) (del Aguila-Pasquel et al., 2014).

TAM plots are the longest running GEM intensive monitoring plots and they are situated on old floodplains of the meandering Tambopata River. TAM-05 is located on an infertile Pleistocene cambisols, whereas TAM-06 is located on a fertile Holocene alluvial

terrace alisols soil types (Aragão et al., 2009; Rowland et al., 2014). These two GEM plots were installed in 2005 and since then both plots were continuously and intensively monitored until 2017. In 2011, a third GEM plot (TAM-09) was installed close to an eddy covariance tower and was monitored until 2015. The rainy season is between December and February and the dry season between May and September Climate (Malhi et al., 2014).

GEM plots in Peruvian Andean forests are located along an elevation gradient from pre-montane to upper montane forests. Many environmental studies have been carried out across this natural laboratory to understand the forest ecosystem functioning along a temperature gradient in tropical montane regions (Malhi et al., 2010). This unique ecosystem is located in Kosñipata Valley of Cusco and Madre de Dios regions that ranges from 595 m asl to 3537 m asl (Girardin et al., 2010; Malhi et al., 2017). Kosñipata Valley spans upper, lower, and pre-montane forests. Six montane plots are located within the Manu National Park, situated at the tree line of Acjanaco forests (ACJ-01), between lower and upper montane forest of Thocha Union (TRU-03, TRU-04, TRU-07, TRU-08), and in pre-montane forests of Tono Valley (TON-01). Six plots are located in the cultural buffer zone of the Manu National Park. Two of them are in the upper montane forests of Wayqecha Biological Station, at 100 m below the local treeline forest (WAY-01) and in a small local valley (ESP-02) (Girardin et al., 2014). Two plots are located in San Pedro lower montane forests above (SPD-01) and below (SPD-02) the cloud base zone, with a mean annual precipitation over 5302 mm $year^{-1}$ (Huaraca Huasco et al., 2014). The last two pre-montane forests (PAN-02, PAN-03) are situated in the Pantiacolla front range of the Andes forests (Malhi et al., 2017). Table 4.2 shows the soil information and climatic information for each montane forest. Farfan-Rios. (2015) listed 1108 tree species and 15 news tree records for Peruvian Flora that spans ~20 km between 800 m and 3625 m elevation across the Kosñipata Valley.

3.1.2 Africa

Across African tropical forest ecosystems, fine root dynamics study was carried out in lowland wet, semi-deciduous, deciduous and pre-montane forests of Ghana, Gabon, and Ethiopia.

3.1.2.1 Ghana: ten lowland plots

In Ghana, the GEM plots span the protected areas of Ankasa Conservation Area (ANK), Bobiri Forest Reserve (BOB), and Kogyae Strict Nature Reserve (KOG) that extend along a precipitation gradient from evergreen southwest forests to dry deciduous southeast forests. Three evergreen ANK wet forests are situated in the extreme southwest of Ghana, close to the Cote d'Ivory border, on oxisols soil types. The rainy season is bimodal, occurring from March to mid-July and from September to November and the dry season extends from December to February (Chiti et al., 2010; Moore et al., 2018). Two Bobiri plots are located in semi-deciduous forests of Ejisu-Juaben district of the Ashanti region with ultisols soil types and on well-drained soils and clay-enriched alluvial subsoil developed or granite (Addo-Danso et al., 2018). The rainy season in Bobiri occurs between April and July, with the minor wet season from September to October, and the dry season occurs from December to mid-March (Ibrahim et al., 2020). The last five Kogyae plots are situated in deciduous forests of the Ashanti region and close to Kumasi city. The permanent plots are located on haplic nitisols and arenosols, with an organic layer between 2.5 cm and 5 cm thick. The KOG plots range from the double rainy season between April and June and with a second period from September to November. Dry season spans from December to March with low humidity (Gvozdevaite et al., 2018).

3.1.2.2 Gabon: four lowland plots

In central semi-deciduous African forest of Gabon, two GEM plots are located in Lope National Park (LPG-01, LPG-02) and two in Ivindo National Park (IVI-01, IVI-02). LPG-01 and LPG-02 are situated on ferrasols soil types and precipitation follows a biannual cycle from March to May and from October to November. There is a long dry season from mid-June to

mid-September (Bush et al., 2020; Wade et al., 2019). The IVI-01 and IVI-02 are situated on cambisols soil types, with two rainy seasons from March to May and from September to December, and with two relatively dry seasons from January to March and from June to August (Koerner et al., 2017; Lamperty et al., 2020).

3.1.2.3 Ethiopia: two pre-montane plots

In western pre-montane forests (1327 and 1500 m asl) of Ethiopia, two small plots of 0.36 ha (60 x 60 m) are located in the Yayu Coffee Forest UNESCO Biosphere Reserve recognised in 2010 (YAY-17, YAY-55). This native coffee reserve is located in Illubabor in the administrative zone of Oromia Regional and biosphere and most characteristics were listed on chapter 4 (Hirons et al., 2018).

3.1.3 South East Asia

3.1.3.1 Malaysia: four lowland plots

In Malaysian Borneo, state of Sabah, there are four lowland mixed dipterocarp old growth forests. In 2011 two one-hectare plots were set up to study the forest ecosystem functioning in Maliau Basin Conservation Area (MLA-01, MLA-02) as a part of the Stability of Altered Forest Ecosystem (SAFE) Project (Ewers et al., 2011). In 2015, two one-hectare plots were selected from the fifty-hectare ForestGEO plot in Danum Valley Conservation Area (DAN-04, DAN-05). Maliau plots are located on Podzol and Danum plots on Orthic Acrisols (Both et al., 2019; Riutta et al., 2018). The region does not have distinct dry and wet seasons and the climate is aseasonal, however there are dry periods and severe droughts that are associated with supra-annual El Niño Southern Oscillation events (Newbery & Lingenfelder, 2009; Rifai et al., 2018).

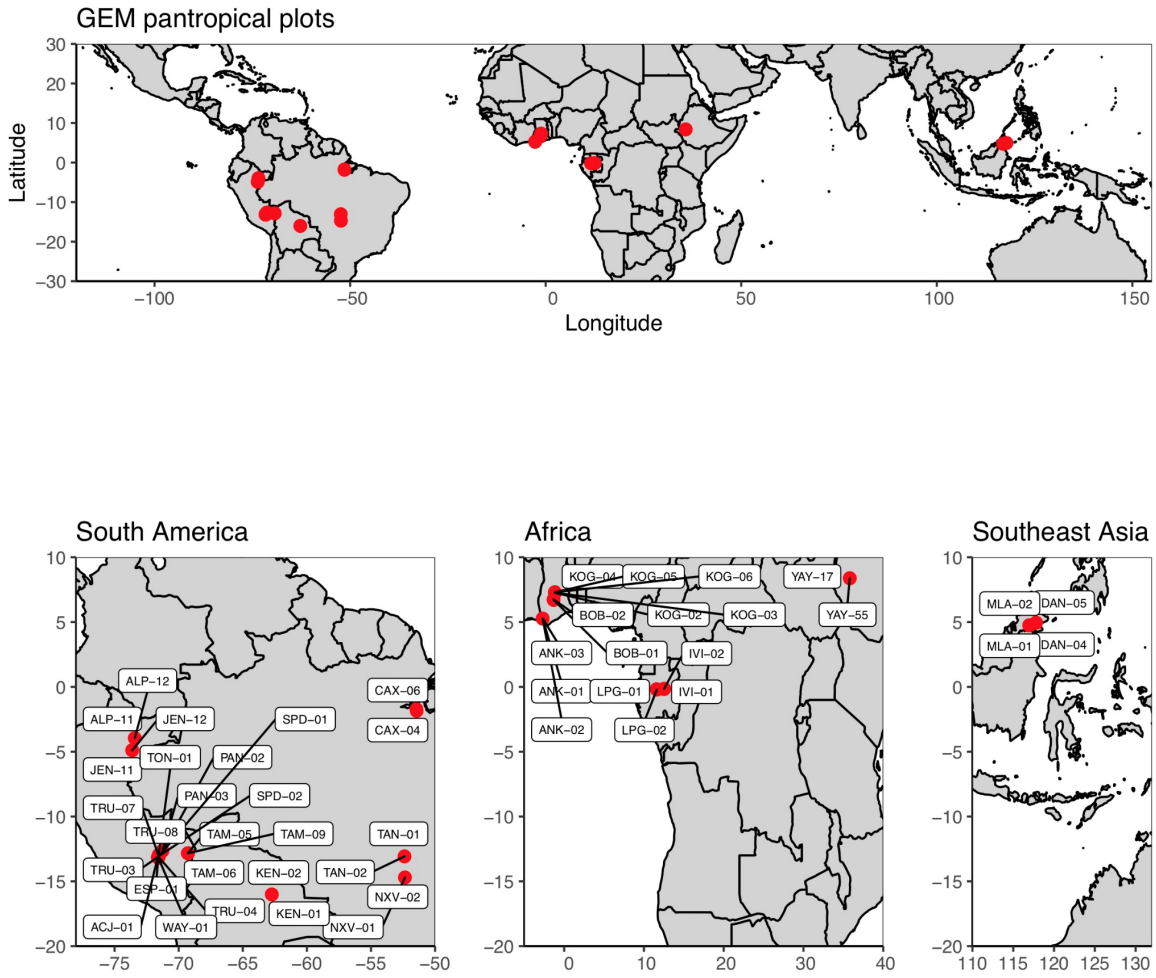


Figure 3.1. Location of fine root dynamics study plots (GEM plots) across South America, Africa, and Asia tropical rainforest ecosystems.

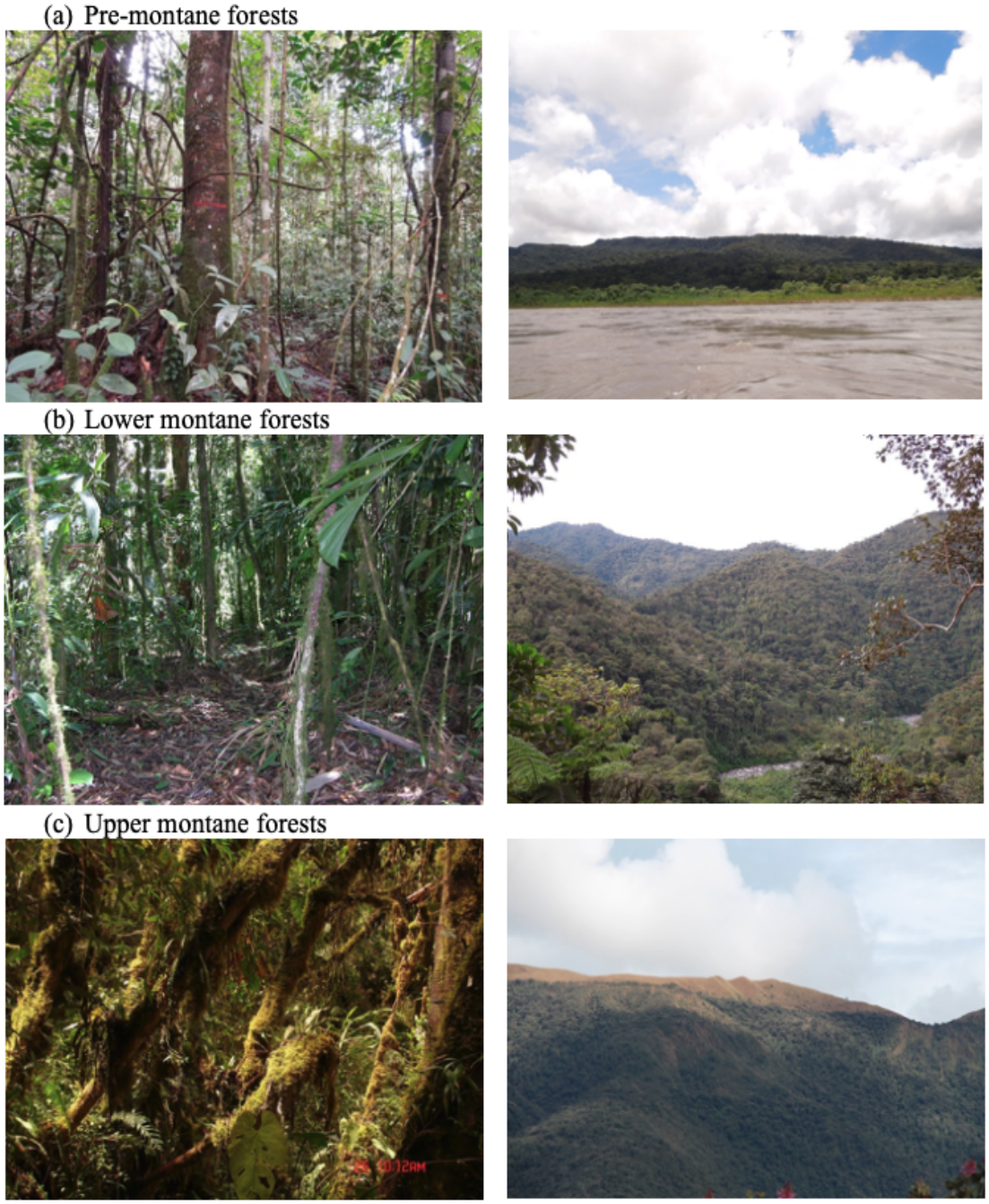


Figure 3.2. Tropical montane forest types in Peruvian Andes, forest understory (left panels) and landscape view (right panels) of Kosñipata Valley transect. (a) pre-montane forests of Pantiacolla (PAN-02, PAN-05). (b) lower montane forests in San Pedro (SPD-01), and (c) upper montane forests in Acjanaco (ACJ-01).

3.2 Project history

This research project was part of a large scientific effort and cooperation between different tropical research projects and networks across tropical regions. The first global research network was the Global Ecosystem Monitoring Ecosystem (GEM: http://gem.tropicalforests.ox.ac.uk/) that focussed on the productivity and carbon cycling using a standard protocol (Marthews et al., 2014). In early 2005, GEM began to record the forest ecosystem functioning across Amazon and Andean forest (Aragão et al., 2009; Girardin et al., 2010). Since 2010 it has expanded to all tropical regions covering different environmental gradients: rainfall in Africa (Moore et al., 2018), logging disturbance in Borneo (Riutta et al., 2018), and elevation and temperature in South America (Malhi et al., 2017, 2021).

Across the lowland forests on the Amazon Forests Inventory Network (RAINFOR: http://www.rainfor.org/) permanent plots were installed for monitoring carbon allocation and carbon cycling using RAINFOR and GEM protocols (Marthews et al., 2014; D. B Metcalfe, Phillips, Baker, & Brienen, 2009) in Peru (del Aguila-Pasquel et al., 2014; Malhi et al., 2014), Bolivia (Araujo-Murakami et al., 2014) and Brazil (da Costa et al., 2014; Rocha et al., 2014). In addition, soil information was recorded following a consistent RAINFOR protocol and then the soil samples were analysed at the National Institute of Amazonian Research (INPA) soil laboratory in Manaus, Brazil (Quesada et al., 2011, 2009). In 2003, permanent plots were set up along a temperature gradient from tree old-growth line forests to pre-montane forests by Andes Biodiversity and Ecosystem Research Group (ABERG; https://www.andesconservation.org/research/). ABERG was led by Professor Miles Silman and Dr. Norma Salinas where I had an opportunity to be part of research team to set up the Peruvian Andes transect plots to record tree diversity (Farfan-Rios et al., 2015; Rapp & Silman, 2012) with Marlene Mamani, William Farfan, Javier Silva, Natividad Raurau, Bryan Valencia, Vicky Huamán, Angela Rozas, Darcy Galiano, Tatiana Boza, Karina Garcia, and Luis Imunda.

To date, many research projects have been conducted on this transect to understand forest ecosystem functioning on aspects such as forest net primary productivity (Girardin et al., 2010, 2014; Huaraca Huasco et al., 2014), plant functional traits (Blonder et al., 2017; Enquist et al., 2017; Goldsmith et al., 2017), and upslope tree migration (Feeley et al., 2011). In addition, the effort of many researchers is now part of natural elevation laboratories to understand biodiversity, ecosystem, ecology, productivity, and biogeochemical cycles (Malhi et al., 2010). In 2013, three new GEM plots were set up for the GEM-TRAIT project in a treeline forest of Manu National Park (Ajanaco), and two plots in Pantiacolla mountain by Beisit Puma, Judith Laupa, Fernando Hancco, Alex Nina, Rudi Chino, Darcy Galiano and many other Peruvian biologist students from Cusco National University of San Antonio Abad located in Cusco region of Peru.

African GEM plots were set up in 2012, covering western African forests precipitation gradient from dry forests of Bobiri Forest Reserve to wet Conservation Area of Ghana (Moore et al., 2018). In Gabon, the establishment and monitoring of permanent plots was supported by core funding from the University of Stirling, Gabon National Parks Agency to research in Ivindo National Park and Lope National Park, and GEM-Trait grant (Aguirre-Gutiérrez et al., 2021; Rifai et al., 2018). In eastern African forests, in Ethiopian montane forests of Yayu Forests Coffee Biosphere Reserve the GEM measurements was led by Ecosystems Limits to Poverty Alleviation in African forest-agriculture Landscapes (ECOLIMITS) project (Morel et al., 2019).

In Malaysian Bornean rainforest, the GEM plots were set up in 2011 led by the Stability of Altered Forest Ecosystem project (SAFE; https://www.safeproject.net/) in partnership with Sabah Forestry Department and Forest Research Centre, Benta Wawasan and the Royal Society South East Asia Rainforest Research to measure forest carbon dynamics across a logging disturbance gradient from old-growth to logged forests (Ewers et al., 2011). Two Bornean old-

growth plots are located in Maliau Basin Conservation Area of Sabah region, where I had the opportunity to set up these two plots, led by Dr. Toby Marthews, Dr. Terhi Riutta, and trained the SAFE Project staff team in the GEM methods. In 2015, two new one-hectare GEM plots were set up in Danum Valley Conservation Area inside a 50-hectare plot that is part of the Center for Tropical Forest Science and The Forest Global Earth Observatory (CTFS-ForestGEO; https://forestgeo.si.edu/what-forestgeo) (Riutta et al., 2021, 2018), led by Dr. Terhi Riutta and Malaysian research assistants; Rostin Jantan, Rohid Kailoh, Suhaini Patik, SAFE Project staff, Danum Valley team, and myself. Finally, my D.Phil study was funded by Peruvian government FONDECYT/CONCYTEC (grant contract number 213-2015-FONDECYT).

3.3 Methods of fine root sampling

Quantifying fine root traits with appropriate techniques is crucial to understand the tropical ecosystem structure and functioning (Green et al., 2005; Yavitt et al., 2011). In this study, I used soil core, ingrowth core, and the combination of screen rhizotron and WinRhizo techniques.

3.3.1 Soil cores

The soil core technique was used to record fine root carbon stock ($Cstock_{fr}$) down to 30 cm soil depth across all the plots in this study. The total number of soil cores was sixteen at each one-hectare plot, in a 20 m by 20 m regular grid, 20 m from the edge of the plot (Figure 3.2a). In some sites, the number of soil cores varied: nine soil cores were collected in some elevations of the Peruvian Andes (TRU-03, TRU-07, TRU-08, and TON-05) and in Ghana (ANK-01, ANK-02, ANK-03), and four soil cores in Ethiopian forests (YAY-17, YAY-55). The size of each soil core was 12 cm in diameter and 30 cm in length. The cores were collected using a double blade shovel (Figure 3.2b). In lowland forests the whole soil layer was considered to be mineral soil while in montane forests the soil layer was separated into organic (OL) and mineral

(ML) layers, the depths of which were recorded. Fine roots were collected manually from the core (Figure 3.2c) for 40 minutes, in 4 × 10-minute time steps, following the GEM protocol (Marthews et al., 2014). The 40-minute fine root technique extraction has been used in Africa, Southeast Asia, and South America tropical forests. This process allows the roots search period to have a reasonable time limit in the field while considering that a small fraction of the fine roots is likely to remain uncollected (Metcalfe et al., 2007). In montane and lowland forests of South America, the 30-cm sample was split into 10 cm layers from which the roots were collected separately, to understand the vertical distribution of fine root carbon stock (Chapter 5). Fine roots were rinsed in water, using fine sieves, to remove soil particles and the root samples were dried in an oven with 70^{o}C until constant mass and weighed with 0.01gram precision.

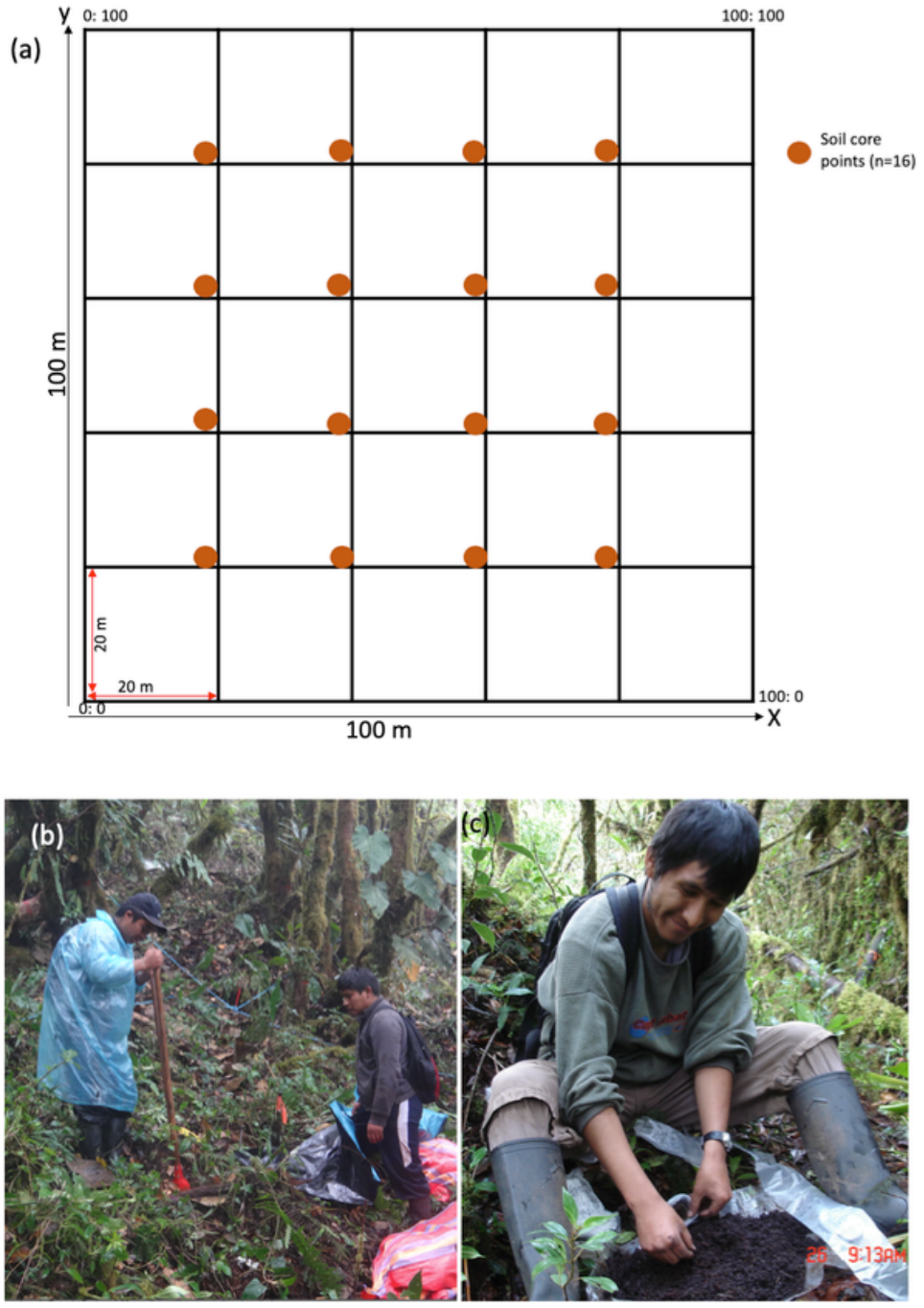


Figure 3.2. (a) Soil core distribution within a one-hectare plot, (b) Peruvian biologist Paul Santos and Yulin Mamani sampling soil cores in WAY-01 upper montane forest, and (c) Johnny Huallpa collecting fine roots at ESP-01 montane forest in Peru.

3.3.2 Ingrowth cores

Ingrowth core bag is usually a mesh bag used to measure fine root productivity in forest ecosystems (Marthews et al., 2014; Metcalfe et al., 2007). The ingrowth core method was used across the plots in this study to estimate fine root productivity and residence time down to 30 cm soil depth (Figure 3.3a). Cylindrical ingrowth cores of 12 cm diameter and 40 cm length were made of plastic wire mesh of 1.5 cm space size, which allowed the regrowth of roots and the movement of soil fauna (Figure 3.3b, c). The soil core excavation holes that were created when collecting the root carbon stock samples were used for installing the cylindrical ingrowth cores, and the newly root-free soil from each hole was then used for filling the ingrowth core (Figure 3.3d, e). Thus, the positioning (Figure. 3.2a) and the sample size of the ingrowth cores was the same as the soil cores. Every three months the ingrowth cores were pulled out to collect fine roots that had grown into the core. Roots were extracted manually, using the same 40-minute fine root search technique that was used with the soil cores (Figure 3.3f, g, h). Fine roots were rinsed in water, using fine sieves, to remove soil particles and the root samples were dried in an oven with 70^{o}C until constant mass and weighed with 0.01gram precision.

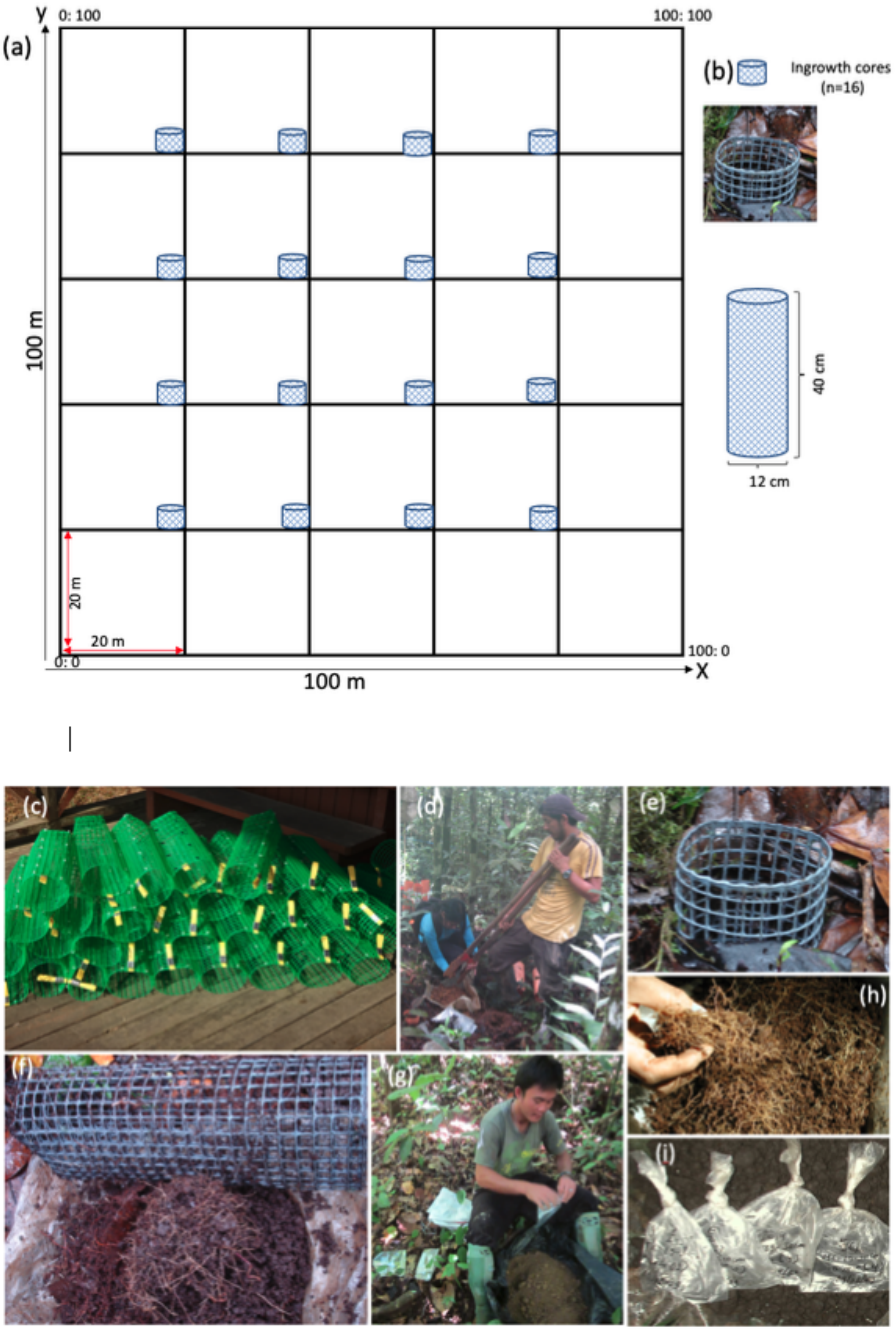


Figure 3.3. (a) Ingrowth core distribution within a one-hectare GEM plot, (b) an ingrowth core with a diameter of 12 cm and length of 40 cm, the top 10 of which is left above the soil surface, (c) ingrowth cores with yellow tags made from plastic wire mesh in Malaysian Danum Valley Conservation Forest, (d) Peruvian biologists Percy Chambi and Judith Laupa Roman digging a soil core to collect fine roots and to install ingrowth cores in pre-montane of Pantiacolla Andes, (e) ingrowth core installed into 30 soil down, with the top 10 cm above the soil surface that helps to locate the core and to pull it out manually every three months, (f) fine root growth after three months, (g) Rostin Jantan harvesting fine roots in Maliau Basin Conservation Area of Malaysia, (h) fine roots after three months in TAM-05, and (h) four bags of fine roots harvested during a 4 × 10 minute manual search from an ingrowth core in ESP-01.

3.3.3 Rhizotrons

Screen rhizotron method was the second technique used for estimating fine root productivity and residence time. In addition, rhizotrons could be used for estimating mortality. Rhizotrons data was collected monthly, while ingrowth cores were collected every three months. The rhizotron method was used in 19 plots in lowland and montane forests of Bolivia, Brazil, and Peru.

Rhizotrons consisted of wooden or metallic support frames and perspex acrylic glass windows with screen size of 21.0 cm width and 29.7 cm height. In upper montane forests, wooden rhizotrons were installed with four supports or legs to improve their steadiness in the thick organic layer, and in lowland forests metallic rhizotrons were installed onto the soil wall by fixing them with long nails. Nine rhizotrons were installed in each one-hectare permanent plot down to 30 cm soil depth (Figure 3.4a). In the lower and upper montane cloud forests, the soil profile was considered to consist of organic and mineral layers, which were recreated as naturally as possible during the rhizotron installation (Figure 3.4b, c, d). The glass face of each rhizotron was separated into three depth layers: 0-10, 10-20 and 20-30 cm, to record vertical variation in fine roots growth and mortality (Figure 3.4e). The rhizotron pits were covered with tarpaulin roofs and the screens were covered with a tight-fitting sponge, to prevent water from collecting into the pits and the roots from being exposed to light. The occurrence of fine roots was recorded by hand tracing over visible roots with permanent markers on transparent A4 acetate sheets placed over the glass face (Figure 3.4f). Information of the root diameter class was recorded through colour coding (>1 mm = black, 1–2 mm = red, 2–3 mm = blue, <4 mm = green) (Figure 3.4g) and the dates of root appearance and disappearance were recorded by numbering each root increment traced.

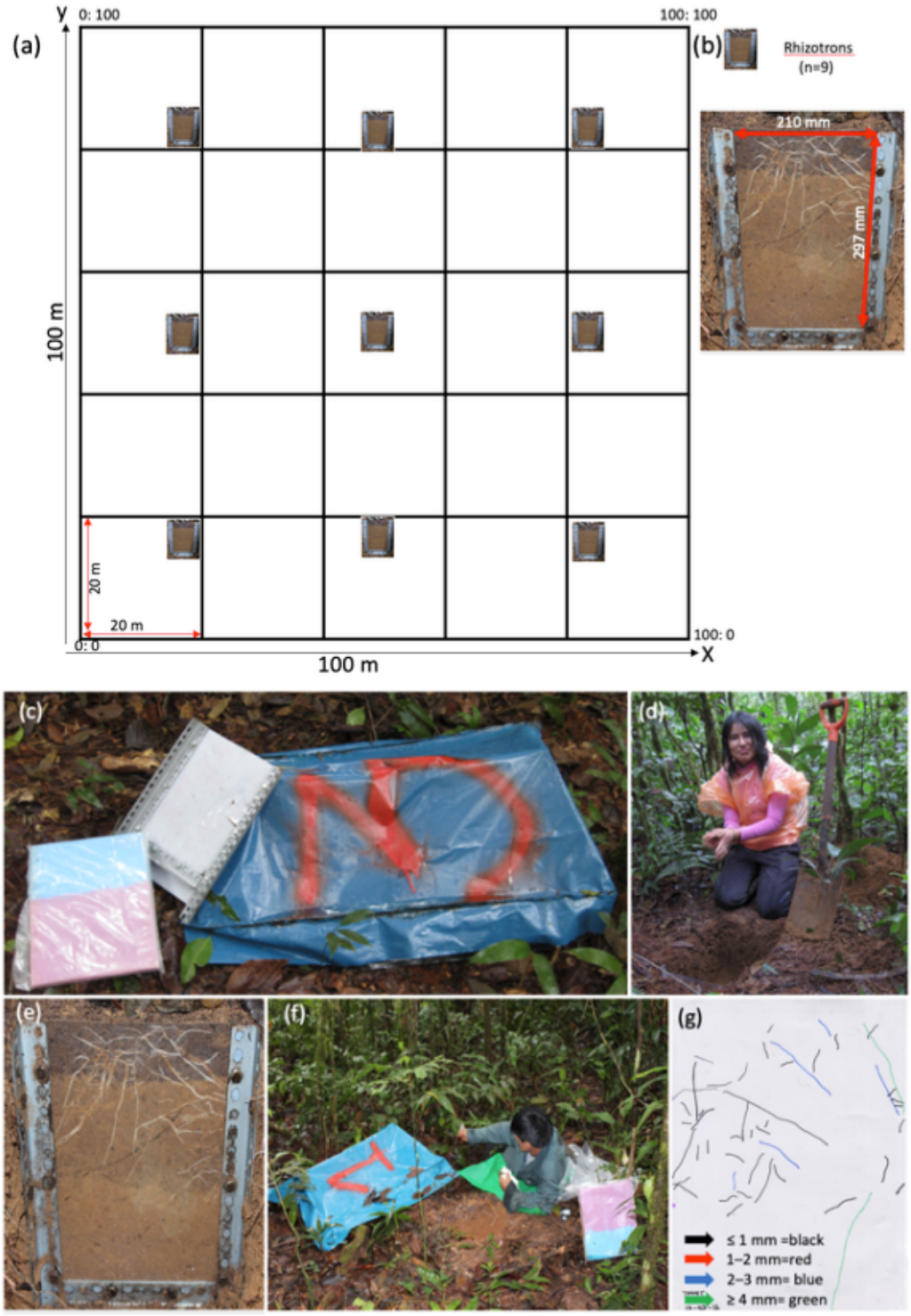


Figure 3.4. (a) Rhizotrons locations within a one-hectare plot, (b) rhizotron with 210 mm width and 297 mm height installed down to 30 cm soil depth, with a distinct organic and mineral soil layers, (c) metallic frame rhizotron and its roof and sponge for covering the screen in PAN-02, (d) Peruvian biologist Judith Laupa Roman installing a rhizotron at PAN-02 plot, (e) fine root growth on the rhizotron screen three months later in PAN-02, (f) Peruvian biologist Fernando Hancco tracing fine roots on rhizotron number one in PAN-03, (g) fine roots traced by hand on an A4-size transparency film.

3.3.4 Root scans for morphological traits

Ingrowth core samples from 15 plots from the Amazonian and Andean forests were used for studying root morphological traits (Chapter 6). Fresh fine roots collected from ingrowth cores were rinsed and placed onto transparent acetate A4 sheets and scanned at 600 dpi using a Canon LiDE 220 scanner. The scanned images were analysed with WinRhizo Pro version 2019 regent instruments inc., Canada (www.regentinstruments.com) to record total fine root length (cm), surface area (cm^2), and volume (cm^3) growth during the three month ingrowth core collection interval, by 0.1 mm diameter classes. Scanned roots were oven dried at 70°C until constant mass to assess fine root productivity, specific root length, specific root surface area, and root tissue density.

3.3.5 Quantification of fine root dynamics and morphological traits

Fine root carbon stock, root phenology of productivity, mortality, residence time, and the fractional allocation of total net primary productivity to the fine roots were quantified to understand the belowground carbon cycle components (Malhi et al., 2021). In addition, fine root morphological traits: length, surface area, volume, specific root length, specific root surface area, and root tissue density were analysed using the WinRhizo software following the methods in the previous studies in tropical forest ecosystem (e.g., Assefa et al., 2018; Girardin et al., 2013; Daniel B. Metcalfe et al., 2008).

3.3.5.1 Fine root carbon stock ($Cstock_{fr}$)

Fine root carbon stock (alive and dead) was defined as the dry mass (g) of roots ≤ 2 mm diameter per the cross-sectional surface area (m^2) of the soil core. A saturating logarithmic curve was fitted to the cumulative fine root dry mass over the 40 min collection time data (Figure 3.3.), where each 10-minute time step formed one data point, showing progressively less fine root mass collected over time (equation 3.1). It was assumed that after 120 minutes

all root fine roots were extracted (Figure 3.3). In the equation, "y" is the cumulative dry fine root mass extracted by the end of each time step, and x is the cumulative search time (minutes) (Marthews et al., 2014, Metcalfe et al., 2007). To assess fine root carbon stock (g C cm^{-2}, kg C m^{-2}, Mg C ha^{-1}), dry biomass was converted into carbon units by assuming a root carbon content of 45% (FRED; roots.ornl.gov; Iversen et al., 2017). To be consistent with other studies that reported fine root dynamics variation in tropical forests, with GEM protocol (e.g., Girardin et al., 2013; Moore et al., 2018).

$$y = a * LN * x + b \quad (3.1)$$

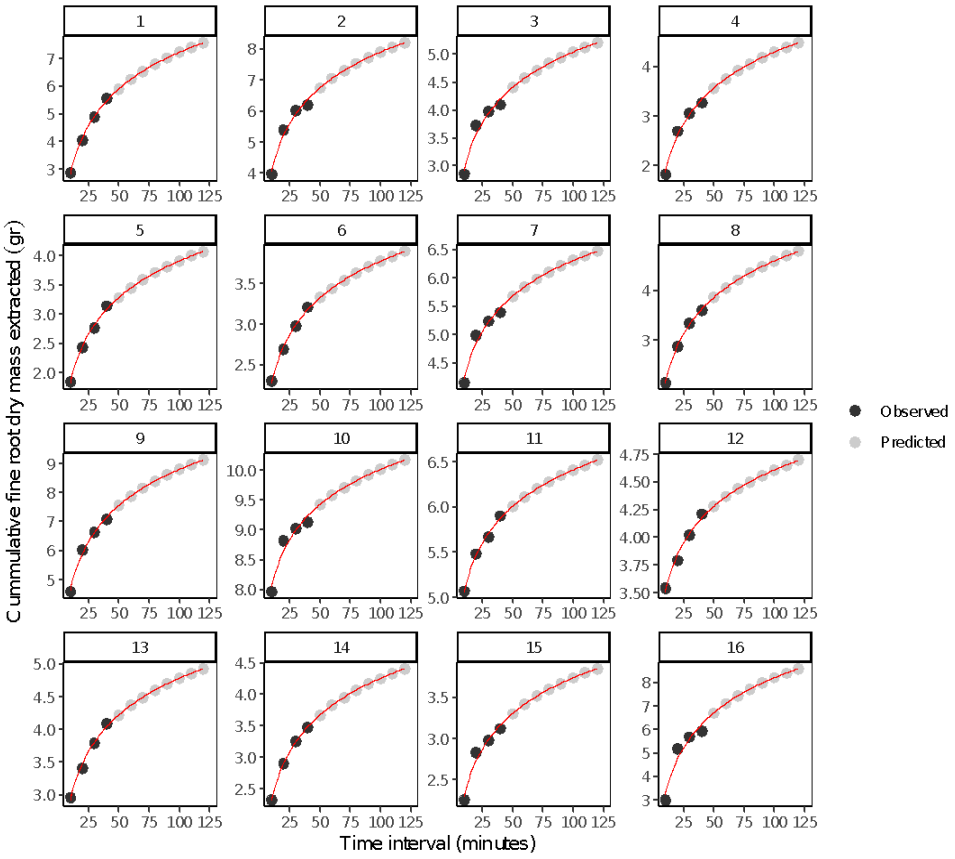


Figure 3.3. Observed cumulative fine root mass (black dots) over a search time of 40 minutes, divided into 4 × 10-minute time steps, and predicted cumulative root mass (grey dots) up to 120 minutes using a logarithmic model (Equation 3.1) in sixteen soil cores in a lowland forest of Tambopata National Reserve, Peru (TAM-05).

3.3.5.2 Fine root primary productivity (NPP_{fr}) using the ingrowth core technique

Fine root productivity was defined as dry mass or roots produced per unit soil ground area and unit time. Root growth collected with ingrowth core technique (NPP_{fr_ic}) every three months was used to assess the mean annual productivity across the tropical forest ecosystems (Chapter 4). Root productivity was calculated using the same saturating logarithmic curve that was fitted for the root biomass data (equation 3.1). The root dry mass was converted to monthly and annual root productivity (Mg C ha^{-1} mo^{-1}; Mg C ha^{-1} yr^{-1}).

3.3.5.3 Fine root productivity and mortality ($Mortality_{fr}$) using the rhizotron technique

Fine root productivity and mortality recorded with rhizotron technique (NPP_{fr_rh}) were analysed to understand the vertical and monthly variation across lowland and montane forests (Chapter 5). Fine root productivity and mortality were assessed using the equations described by Bernier & Robitaille, (2004) (equation 3.2; equation 3.3), previously used in the Amazonian-Andean root dynamic studies (Girardin et al., 2013; Metcalfe et al., 2007). The monthly fine root productivity and mortality were calculated following the number of roots contacting and disappearing on the rhizotron screen each month, by diameter classes. Fine roots were recorded as alive at their first appearance, and then in future sessions if they were not found, they were considered as dead (mortality).

The total cross-sectional surface area of intersecting fine roots (CSA_{fr}, mm2) was calculated using the equation 3.2, where r is the root radius (mm). Any roots that branched after the first recorded contact with the rhizotron observation screen were not counted in the future sessions. Total surface cross-sectional surface area was used to calculate the monthly fine root productivity and mortality (GM_{fr}) (equation 3.3.). Equation 3.3 shows the fine root tissue density (D_{fr}, g mm^{-3}: assumed constant equal to 0.00029), soil coarse fraction particles > 2mm (fc, in forest soil is equal to 0), angle of the rhizotron observation screen relative to the ground (α), ground angle relative to the horizontal (γ), and width of the rhizotron observation screen

(W, mm). The 10^4 value converts mm^2 ground area into one hectare, and grams into megagrams. The multiplication factor 2 on equation 3.3 is used because roots can only intersect with the rhizotron screen from the soil side. It was assumed that if there was soil on both sides of the screen, rather than an empty space to allow for measurement and observation then an equal number of roots would intersect from both sides.

$$CSA_{fr} = \frac{\pi^2 * \Sigma r^2}{\sqrt{2}} \quad (3.2)$$

$$GM_{fr} = 2 * 10^4 * D_{fr} * (1 - fc) * CSA_{fr} * \frac{\sin\alpha * \cos\gamma}{W} \quad (3.3)$$

3.3.5.4 Fine root residence time (RT_{fr})

Root residence time is defined as the length of time a carbon atom spends as part of the living fine roots tissue (Galbraith et al., 2013; Telles et al., 2003). RT_{fr} was calculated by dividing the total fine root carbon stock by annual rate of productivity (equation 3.4) (Girardin et al., 2013). The mean residence time (days, months, years) of fine roots is the reciprocal of turnover rate (Assefa et al., 2017; Tingey et al., 2000).

$$RT_{fr} = Cstock_{fr} / NPP_{fr} \quad (3.4)$$

Fine root carbon stock ($Cstock_{fr}$) estimates were derived from the soil cores. Net primary productivity (NPP_{fr}) data was recorded with two methods: fine root productivity with ingrowth (NPP_{fr_ic}) and with rhizotrons technique (NPP_{fr_rh}).

3.3.5.5 Fractional carbon allocation of net primary productivity to fine roots ($Allocation_{fr}$)

Carbon allocation into fine roots is considered to be an investment for soil nutrient and water acquisition. Fractional allocation of total net primary productivity (NPP_{total}, equation 3.5) to fine root productivity was calculated by dividing the NPP_{fr} recorded only with ingrowth core technique by total ecosystem net primary productivity (equation 3.6). NPP_{total} is the sum of aboveground productivity (NPP_{AG}): canopy productivity (estimated from canopy litterfall), wood productivity (stem and coarse wood productivity of stem ≥ 10 cm diameter at breast height), and belowground productivity (NPP_{BG}): coarse and fine roots.

$$NPP_{total} = NPP_{AG} + NPP_{BG} \quad (3.5)$$

$$Allocation_{fr} = NPP_{total}/NPP_{fr} \quad (3.6)$$

3.3.5.6 Fine root morphological traits

Fine root morphological traits were categorised into length (LEN_{fr}, cm), surface area (SA_{fr}, cm^2), volume (VOL_{fr}, cm^3), specific root length (SRL), specific surface area (SRA), and root tissue density (RTD) features. The data were divided into twenty 0.1 mm diameter classes for the fine roots ≤ 2 mm, to understand the annual growth of total LEN_{fr} (km m^{-2} yr^{-1}), SA_{fr} (m^2 m^{-2} yr^{-1}), and VOL_{fr} (cm^3 m^{-2} yr^{-1}). Annual LEN_{fr} growth was divided by annual average NPP_{fr_ic} to calculate SRL (km kg^{-1}) (equation 3.7) and SA_{fr} growth was divided by NPP_{fr_ic} to calculate SRL (m^2 kg^{-1}) (equation 3.8)**.** Annual average NPP_{fr_ic} was divided by VOL_{fr} to calculate RTD (g cm^{-3}) (equation 3.9).

$$SRL = LEN_{fr}/NPP_{fr_ic} \quad (3.7)$$

$$SRA = SA_{fr}/NPP_{fr_ic} \quad (3.8)$$

$$RTD = NPP_{fr_ic} / VOL_{fr} \quad (3.9)$$

3.4 Soil chemical and physical properties

Soil properties across the GEM monitoring plots were assessed with pits and soil cores (Figure 3.5). A soil pit was situated at a representative spot a few metres outside the plot boundary to reduce disturbance to trees and understory plants. The pit size was with 1.5 m length, 1.5 m width and 2.0 m depth. Bulk density samples were collected from the pit wall, using designed container-rings of known volume. Soil cores were collected using an undisturbed soil sampler on five points in the middle and at four corners of each one-hectare plot. Samples were collected from soil depths of 0-5 cm, 5-10 cm, 10-20 cm, and 20-30 cm. The soil sampling protocol, lab analysis, and soil classification are in detail described in (Quesada et al., 2009). Soil data were collected from all sites to a consistent RAINFOR protocol and analyzed to a common protocol either at the INPA soil laboratory in Manaus, Brazil (samples from Brazil, Bolivia, and Peru) or at the University of Leeds (all other samples).



Figure 3.5. (a) Soil pit at PAN-03 plot digging by a Peruvian biologist Marco Cusipaucar, (b) MLA-01 pit digging by Malaysian research assistants, the flagging tape marking the undisturbed side to be used for the sampling, (c) Jimmy Chambi at ACJ-01 pit, and (d) Erick Oblitas in Acjanaco tree line forest plot pit sampling soil sample to assess the soil nutrients content.

3.5 Climatic variables

Climatic variables were collected from automatic weather stations (Skye Instruments, Llandrindod, UK) that were installed in clearing areas close to the plots. The weather stations recorded the main climatic variables of air temperature, relative humidity, precipitation, solar radiation, and wind speed every 30 minutes. Monthly soil temperature and moisture were also measured in 25 points of each one-hectare plot (middle of each subplot) and close to each

rhizotron. Soil temperature was measured with Testo 926 thermometer, and volumetric soil water content was measured with a water content reflectometer CS616 sensor (HydroSense, CampbellScientific), down to 20 cm soil depth in montane forests and at 12 cm soil depth in lowland forests.



Figure 3.6. (a) Automatic weather station installed in Pantiacolla mountain close to PAN-03 plot, (b) Peruvian biologists Judith Laupa and Fernando Hancco installing a weather station at Pantiacolla lodge, (c) water content reflectometer CS616 and soil temperature sensors in ESP-01, (d) Ghanian GEM team lead by Sam Moore and Yadvinder Malhi at a newly installed weather station (photo by Sam Moore).

3.6 Statistical analysis of research chapters

To understand the main drives of fine root carbon stock, carbon dynamics, seasonal variation, morphological dynamics, and morphological traits across tropical forests were conducted with different statistical analyses. Each research chapter (4, 5, and 6) was analysed independently to answer the main and specific questions. To identify the main drivers of fine root carbon stock and dynamics across pantropical forest ecosystems (Chapter 4). I conducted multiple regression analyses, using generalised additive models (GAM), with soil properties and climatic variables as potential explanatory variables. Lowland and montane forests were modelled separately, as their relationship with environmental variables are likely to be different. First, I conducted a principal component analysis (PCA) on soil variables, separately for lowland and montane forest, to reduce the dimensionality of soil predictors (sand, silt, clay, pH, nitrogen, carbon-nitrogen ratio, phosphorus, aluminium, calcium, potassium, magnesium, sodium, and soil cation exchange capacity) and to identify the most orthogonal soil properties. The soil properties with the highest loadings on the first four PCA axes were selected as potential explanatory variables in the regression models (Chapter 4 and Chapter 6). In addition to soil properties, the climatic variables mean annual precipitation, maximum cumulative water deficit, and mean annual temperature were tested as explanatory variables. Fine root carbon stock ($Cstock_{fr}$), net primary productivity of fine roots (NPP_{fr}), and fine root residence time (RT_{fr}) were modelled using Gamma distribution (values are positive, variance increases with increasing mean) with a log link function, whereas fractional allocation of total net primary productivity to the fine roots ($Allocation_{fr}$) was modelled using beta distribution (values between zero and one). First, I the full model was fitted, and variables were dropped until the combination of explanatory variables that best explained each fine root dynamics component was found. Candidate models were compared using Akaike's information criterion, corrected for small samples.

The vertical and temporal variation of fine root dynamics in Amazonian and Andean forests (Chapter 5) were recorded using the rhizotron (NPP_{fr_rh}) and ingrowth core ($NPPf_{r_ic}$) techniques. Comparison of total variation of NPP_{fr_rh} and NPP_{fr_ic} was conducted by Passing-Bablok non-parametric regression analysis as a robust and appropriate model of method comparison (Bilic-Zulle et al., 2011). The vertical distribution of $Cstock_{fr}$, $NPP_{fr,}$ and RT_{fr} from top soil to 30 cm depth by 10 cm layers was described by fitting a linear model with depth. To facilitate the comparison of the vertical pattern among sites with different total fine root productivity, we also fitted a linear model with depth and scaled productivity, where the root productivity of the topsoil layer was set to one. Generalised additive model analyses were performed to examine the relationships between root dynamics and elevation, precipitation and soil organic layer thickness at annual and seasonal scales.

Chapter 6 focused on the spatial variation of root morphological dynamics (fine root length growth and fine root surface area growth) and traits (specific root length and specific root surface area) from lowland to upper montane forests. Generalised additive models were conducted to understand the effect of elevation and soil properties on fine root morphological dynamics and traits. I conducted a PCA to reduce the dimensionality of soil properties and to identify the most orthogonal soil properties for the GAM model. In addition, to examining fine roots as an entity, I examined the relationship between root morphological variables and environmental variables separately by 0.1 mm diameter classes. I calculated the Pearson correlation coefficient for each pair of root and environmental variable by diameter class, each plot forming one observation. After obtaining the correlation coefficient for each diameter class, I fitted a GAM model with the correlation coefficient as the response variable and root diameter class as the explanatory variable to describe how the strength and direction of the relationship between root variables and abiotic variables change depending on root size.

3.7 References

Addo-Danso, S. D., Prescott, C. E., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Guy, R. D., … Malhi, Y. (2018). Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. *Biotropica*, *50*(4), 606–615. https://doi.org/10.1111/btp.12556

Aguirre-Gutiérrez, J., Rifai, S., Shenkin, A., Oliveras, I., Bentley, L. P., Svátek, M., … Malhi, Y. (2021). Pantropical modelling of canopy functional traits using Sentinel-2 remote sensing data. *Remote Sensing of Environment*, *252*(October). https://doi.org/10.1016/j.rse.2020.112122

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Araujo-Murakami, A., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., … Malhi, Y. (2014). The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecology & Diversity*, *7*(1–2), 55–69. https://doi.org/10.1080/17550874.2013.798364

Assefa, D., Godbold, D. L., Belay, B., Abiyu, A., & Rewald, B. (2018). Fine Root Morphology, Biochemistry and Litter Quality Indices of Fast- and Slow-growing Woody Species in Ethiopian Highland Forest. *Ecosystems*, *21*(3), 482–494. https://doi.org/10.1007/s10021-017-0163-7

Assefa, D., Rewald, B., Sandén, H., & Godbold, D. L. (2017). Fine Root Dynamics in Afromontane Forest and Adjacent Land Uses in the Northwest Ethiopian Highlands. *Forests*, *8*(7), 249. https://doi.org/10.3390/f8070249

Bernier, P. Y., & Robitaille, G. (2004). A plane intersect method for estimating fine root productivity of trees from minirhizotron images. *Plant and Soil*, *265*(1–2), 165–173. https://doi.org/10.1007/s11104-005-0056-y

Bilic-Zulle, L. (2011). Comparison of methods: Passing and Bablok regression. *Biochemia Medica*, *21*(1), 49–52. https://hrcak.srce.hr/64499

Blonder, B., Salinas, N., Patrick Bentley, L., Shenkin, A., Chambi Porroa, P. O., Valdez Tejeira, Y., … Malhi, Y. (2017). Predicting trait-environment relationships for venation networks along an Andes-Amazon elevation gradient. *Ecology*, *98*(5), 1239–1255. https://doi.org/10.1002/ecy.1747

Both, S., Riutta, T., Paine, C. E. T., Elias, D. M. O., Cruz, R. S., Jain, A., … Burslem, D. F. R. P. (2019). Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytologist*, *221*(4), 1853–1865. https://doi.org/10.1111/nph.15444

Bush, E. R., Jeffery, K., Bunnefeld, N., Tutin, C., Musgrave, R., Moussavou, G., … Abernethy, K. (2020). Rare ground data confirm significant warming and drying in western equatorial Africa. *PeerJ*, *8*, e8732. https://doi.org/10.7717/peerj.8732

Chiti, T., Certini, G., Grieco, E., & Valentini, R. (2010). The role of soil in storing carbon in tropical rainforests: The case of Ankasa Park, Ghana. *Plant and Soil*, *331*(1), 453–461. https://doi.org/10.1007/s11104-009-0265-x

da Costa, A. C. L., Metcalfe, D. B., Doughty, C. E., de Oliveira, A. A. R., Neto, G. F. C., da Costa, M. C., … Malhi, Y. (2014). Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest. *Plant Ecology & Diversity*, *7*(1–2), 7–24. https://doi.org/10.1080/17550874.2013.798366

de Farias, J., Marimon, B. S., de Carvalho Ramos Silva, L., Petter, F. A., Andrade, F. R., Morandi, P. S., & Marimon-Junior, B. H. (2016). Survival and growth of native Tachigali vulgaris and exotic Eucalyptus urophylla×Eucalyptus grandis trees in degraded soils with

biochar amendment in southern Amazonia. *Forest Ecology and Management*, *368*, 173–182. https://doi.org/10.1016/j.foreco.2016.03.022

del Aguila-Pasquel, J., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Girardin, C. A. J., Chung Gutierrez, J. A., … Malhi, Y. (2014). The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology & Diversity*, *7*(1–2), 71–83. https://doi.org/10.1080/17550874.2013.798365

Doughty, C. E., Metcalfe, D. B., da Costa, M. C. L., de Oliveira, A. A. R., Neto, G. F. C., Silva, J. A., … Malhi, Y. (2014). The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil. *Plant Ecology & Diversity*, *7*(1–2), 41–53. https://doi.org/10.1080/17550874.2013.798367

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huaraca Huasco, W., … Malhi, Y. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541), 78–82. https://doi.org/10.1038/nature14213

Enquist, B. J., Bentley, L. P., Shenkin, A., Maitner, B., Savage, V., Michaletz, S., … Malhi, Y. (2017). Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Global Ecology and Biogeography*, *26*(12), 1357–1373. https://doi.org/10.1111/geb.12645

Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., … Turner, E. C. (2011). A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1582), 3292–3302. https://doi.org/10.1098/rstb.2011.0049

Farfan-Rios, W., Garcia-Cabrera, K., Salinas, N., Raurau-Quisiyupanqui, M. N., & Silman, M. R. (2015). Lista anotada de árboles y afines en los bosques montanos del sureste peruano: la importancia de seguir recolectando TT - An annotated checklist of trees and relatives in tropical montane forests from southeast Peru: the importance of continue collecting. *Revista Peruana de Biología*, *22*(2), 145–174. http://www.scielo.org.pe/scielo.php?script=sci_arttext&pid=S1727-99332015000200004&lang=pt

Feeley, K. J., Silman, M. R., Bush, M. B., Farfan, W., Cabrera, K. G., Malhi, Y., … Saatchi, S. (2011). Upslope migration of Andean trees. *Journal of Biogeography*, *38*(4), 783–791. https://doi.org/10.1111/j.1365-2699.2010.02444.x

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D. A., Doughty, C. E., Fisher, R. A., … Lloyd, J. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, *6*(1), 139–157. https://doi.org/10.1080/17550874.2013.770578

Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082

Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., … Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*(12), 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x

Goldsmith, G. R., Bentley, L. P., Shenkin, A., Salinas, N., Blonder, B., Martin, R. E., … Malhi, Y. (2017). Variation in leaf wettability traits along a tropical montane elevation gradient. *New Phytologist*, *214*(3), 989–1001. https://doi.org/10.1111/nph.14121

Green, J. J., Dawson, L. A., Proctor, J., Duff, E. I., & Elston, D. A. (2005). Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. *Plant and Soil*, *276*(1–2), 23–32. https://doi.org/10.1007/s11104-004-0331-3

Gvozdevaite, A., Oliveras, I., Domingues, T. F., Peprah, T., Boakye, M., Afriyie, L., … Malhi, Y. (2018). Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–savanna boundaries in Ghana and Brazil. *Tree Physiology*, *38*(12), 1912–1925. https://doi.org/10.1093/treephys/tpy117

Hirons, M., Robinson, E., McDermott, C., Morel, A., Asare, R., Boyd, E., … Norris, K. (2018). Understanding Poverty in Cash-crop Agro-forestry Systems: Evidence from Ghana and Ethiopia. *Ecological Economics*, *154*, 31–41. https://doi.org/10.1016/j.ecolecon.2018.07.021

Honorio, E. N., Pennington, T. R., A, F. L., Nebel, Rg., & Baker, T. R. (2008). Análisis de la composición florística de los bosques de Jenaro Herrera, Loreto, Perú -Analysis of the floristic composition of the forests of Jenaro Herrera, Loreto, Peru. *Rev. Peru. Biol.*, *15*(1), 53–60.

Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042

Ibrahim, F., Adu-Bredu, S., Addo-Danso, S. D., Duah-Gyamfi, A., Manu, E. A., & Malhi, Y. (2020). Patterns and controls on fine-root dynamics along a rainfall gradient in Ghana. *Trees*, 1–13. https://doi.org/10.1007/s00468-020-01970-3

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., … Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26. https://doi.org/10.1111/nph.14486

Koerner, S. E., Poulsen, J. R., Blanchard, E. J., Okouyi, J., & Clark, C. J. (2017). Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *Journal of Applied Ecology*, *54*(3), 805–814. https://doi.org/10.1111/1365-2664.12798

Lamperty, T., Zhu, K., Poulsen, J. R., & Dunham, A. E. (2020). Defaunation of large mammals alters understory vegetation and functional importance of invertebrates in an Afrotropical forest. *Biological Conservation*, *241*, 108329. https://doi.org/10.1016/j.biocon.2019.108329

Malhi, Y., del Aguilla-Pasquell, J., Metcalfe, D. B., Phillips, O. L., Farfan-Rios, W., Silman, M., … Farfán Amézquita, F. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., … Phillips, O. L. (2015). The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology*, *21*(6), 2283–2295. https://doi.org/10.1111/gcb.12859

Malhi, Y., Farfán Amézquita, F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., … Phillips, O. L. (2014). The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology and Diversity*, *7*(1–2), 85–105. https://doi.org/10.1080/17550874.2013.820805

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E. O. C., Rifai, S. W., … Phillips, O. L. (2021). The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. *Biological Conservation*, *253*, 108889. https://doi.org/10.1016/j.biocon.2020.108889

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P., & Saatchi, S. (2010). Introduction: Elevation gradients in the tropics: Laboratories for ecosystem ecology and global change research. *Global Change Biology*, *16*(12), 3171–3175. https://doi.org/10.1111/j.1365-

2486.2010.02323.x

Marimon, B. S., Marimon-Junior, B. H., Feldpausch, T. R., Oliveira-Santos, C., Mews, H. A., Lopez-Gonzalez, G., … Phillips, O. L. (2014). Disequilibrium and hyperdynamic tree turnover at the forest–cerrado transition zone in southern Amazonia. *Plant Ecology & Diversity*, *7*(1–2), 281–292. https://doi.org/10.1080/17550874.2013.818072

Marthews, T. R., Riutta, T., Menor, I. O., Urrutia, R., Moore, S., Metcalfe, D., … Networks, C. R. and colleagues from the R. and G. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0, 121.

Metcalfe, D. B., Williams, M., Aragão, L. E. O. C., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., … Meir, P. (2007). A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. *New Phytologist*, *174*(3), 697–703. https://doi.org/10.1111/j.1469-8137.2007.02032.x

Metcalfe, D. B, Phillips, O., Baker, T., & Brienen, R. (2009). Measuring Tropical Forest Carbon Allocation And Cycling. *RAINFOR Field Manual*, (June), 1–24.

Metcalfe, Daniel B., Meir, P., Aragão, L. E. O. C., da Costa, A. C. L., Braga, A. P., Gonçalves, P. H. L., … Williams, M. (2008). The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, *311*(1–2), 189–199. https://doi.org/10.1007/s11104-008-9670-9

Moore, S., Adu-Bredu, S., Duah-Gyamfi, A., Addo-Danso, S. D., Ibrahim, F., Mbou, A. T., … Malhi, Y. (2018). Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. *Global Change Biology*, *24*(2), e496–e510. https://doi.org/10.1111/gcb.13907

Morel, A. C., Adu Sasu, M., Adu-Bredu, S., Quaye, M., Moore, C., Ashley Asare, R., … Malhi, Y. (2019). Carbon dynamics, net primary productivity and human-appropriated net primary productivity across a forest–cocoa farm landscape in West Africa. *Global Change Biology*, *25*(8), 2661–2677. https://doi.org/10.1111/gcb.14661

Newbery, D. M., & Lingenfelder, M. (2009). Plurality of tree species responses to drought perturbation in Bornean tropical rain forest. *Plant Ecology*, *201*(1), 147–167. https://doi.org/10.1007/s11258-008-9533-8

Neyret, M., Bentley, L. P., Oliveras, I., Marimon, B. S., Marimon-Junior, B. H., Almeida de Oliveira, E., … Malhi, Y. (2016). Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients in light of community assembly. *Ecology and Evolution*, *6*(16), 5674–5689. https://doi.org/10.1002/ece3.2281

Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., & Czimczik, C. I. (2011). Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences*, *8*(6), 1415–1440. https://doi.org/10.5194/bg-8-1415-2011

Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., … Paiva, R. (2009). Chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences Discussions*, *6*(2), 3923–3992. https://doi.org/10.5194/bgd-6-3923-2009

Rapp, J., & Silman, M. (2012). Diurnal, seasonal, and altitudinal trends in microclimate across a tropical montane cloud forest. *Climate Research*, *55*(1), 17–32. https://doi.org/10.3354/cr01127

Rifai, S. W., Girardin, C. A. J., Berenguer, E., del Aguila-Pasquel, J., Dahlsjö, C. A. L., Doughty, C. E., … Malhi, Y. (2018). ENSO Drives interannual variation of forest woody growth across the tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1760), 20170410. https://doi.org/10.1098/rstb.2017.0410

Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M., … Ewers, R. M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology*, *24*(7), 2913–2928.

https://doi.org/10.1111/gcb.14068

Rowland, L., Malhi, Y., Silva-Espejo, J. E., Farfán-Amézquita, F., Halladay, K., Doughty, C. E., … Phillips, O. L. (2014). The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest. *Oecologia*, *174*(1), 295–306. https://doi.org/10.1007/s00442-013-2766-9

Sotta, E. D., Veldkamp, E., Guimarães, B. R., Paixão, R. K., Ruivo, M. L. P., & Almeida, S. S. (2006). Landscape and climatic controls on spatial and temporal variation in soil CO2 efflux in an Eastern Amazonian Rainforest, Caxiuanã, Brazil. *Forest Ecology and Management*, *237*(1–3), 57–64. https://doi.org/10.1016/j.foreco.2006.09.027

Telles, E. de C. C., de Camargo, P. B., Martinelli, L. A., Trumbore, S. E., da Costa, E. S., Santos, J., … Oliveira, R. C. (2003). Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles*, *17*(2). https://doi.org/10.1029/2002GB001953

Tingey, D. T., Phillips, D. L., & Johnson, M. G. (2000). Elevated CO2 and conifer roots: effects on growth, life span and turnover. *New Phytologist*, *147*(1), 87–103. https://doi.org/10.1046/j.1469-8137.2000.00684.x

Waddell, J. C., & Crampton, W. G. R. (2020). Environmental correlates of circannual breeding periodicity in a multi-species assemblage of Amazonian electric fishes. *Environmental Biology of Fishes*, *103*(3), 233–250. https://doi.org/10.1007/s10641-020-00950-3

Wade, A. M., Richter, D. D., Medjibe, V. P., Bacon, A. R., Heine, P. R., White, L. J. T., & Poulsen, J. R. (2019). Estimates and determinants of stocks of deep soil carbon in Gabon, Central Africa. *Geoderma*, *341*, 236–248. https://doi.org/10.1016/j.geoderma.2019.01.004

Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., & Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecology*, *36*(4), 433–445. https://doi.org/10.1111/j.1442-9993.2010.02157.x

3.8 Supplementary material

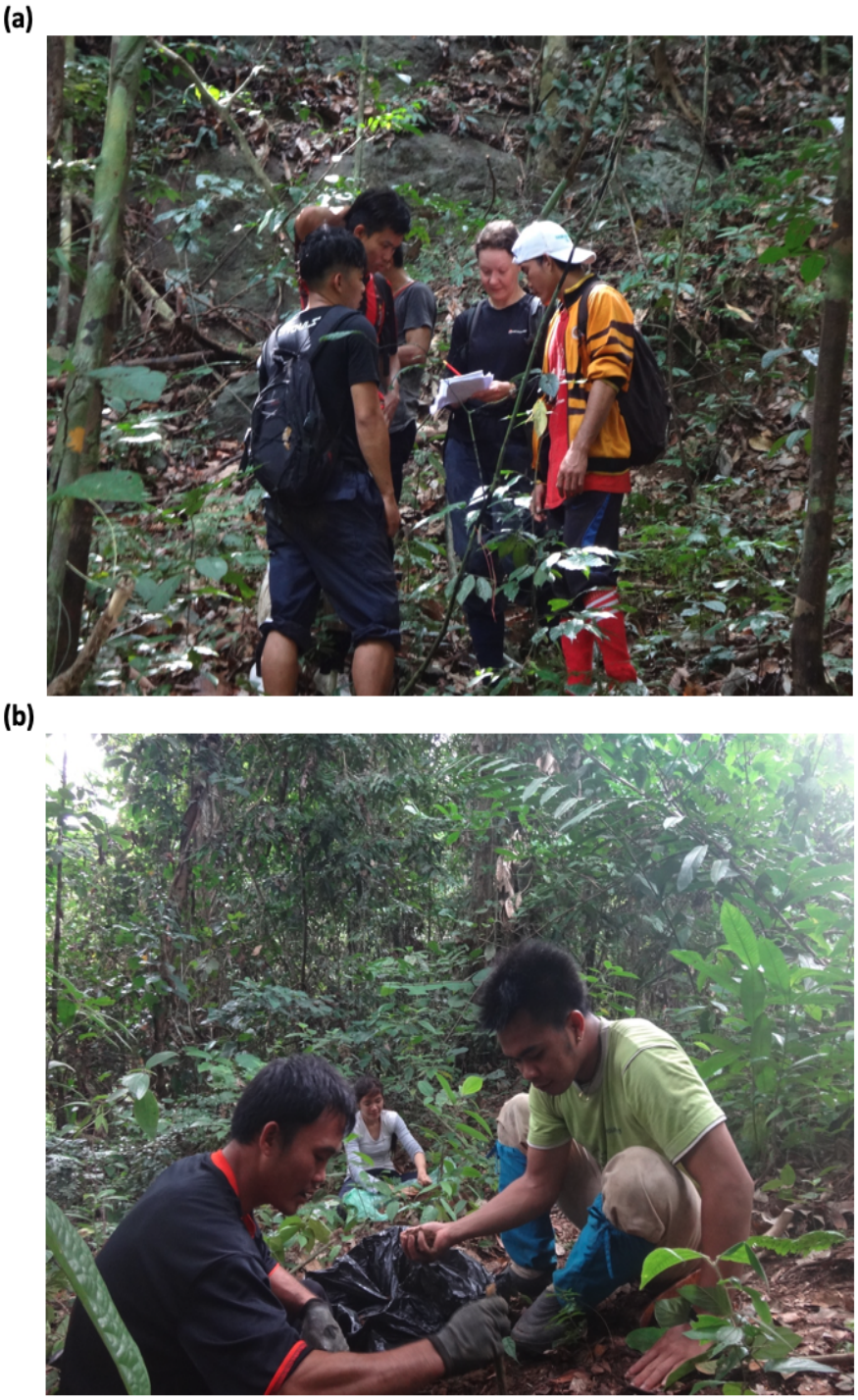


Figure S3.1. (a) Malaysian GEM team lead Dr. Terhi Riutta, Rostin Jantan, and Danum Valley researcher assistants are marking the DAN-04 plot corners in 2015, at Danum Valley 50 ha plot. (b) Malaysian carbon team members Rostin Jantan, Rohid Kailoh, and Suhaini Patik are installing ingrowth cores in 2015.



Figure S3.2. (a) Ghanian GEM team lead Dr. Sam Moore and local researchers. (c) Ethiopian carbon team led by Dr. Alexandra Morel and local researchers.

(a)



(b)



Figure S3.3. (a) Peruvian GEM team at Pantiacolla lodge, after a successful three-month fieldwork campaign across upper montane and pre-montane forests, led by Biologists Beisit Puma and Melania Laupa in April 2013. (b) Peruvian carbon team biologists in Tres Cruces (Peru), at the beginning of Andean transect of Trocha Union in February 2013.

Chapter 4: Fine root dynamics across pantropical rainforest ecosystems

This chapter is one of the largest studies of fine root carbon stock and dynamics across tropical rainforest ecosystems spanning three continents: South America, Africa, and Asia. I collected data from tropical lowland (moist, semi-deciduous, and deciduous) and montane (pre-montane, lower montane, upper montane) forest types. This chapter provides estimates on fine root carbon stock, productivity, residence time, and fractional carbon allocation of total net primary productivity to the fine roots in lowland and montane forests for 47 plots in seven countries. In addition, the paper explores how climatic and soil properties control the variation in fine root carbon stock and dynamics in lowland and montane forests. One of the major advantages of this paper is that all the root and soils data were collected using standard protocols. This study contributes to our understanding of tropical belowground carbon cycle ecology, which plays a key role in ecosystem functioning.

I conceived this paper together with my supervisors, and lead on data processing, analysis and writing. I directly collected data from the Peruvian and Malaysian sites, and played a leading role in developing the protocol and training data collectors in the other sites. Other co-authors collected and provided data from the other field sites. Sami Rifai helped in modelling the results. This paper was submitted to *Global Change Biology* in November 2020, and was accepted for publication in March 2021.

Title: Fine root dynamics across pantropical rainforest ecosystems

Authors: Walter Huaraca Huasco[1*], Terhi Riutta[1], Cécile. A. J. Girardin[1], Fernando Hancco Pacha[2], Beisit L. Puma Vilca[2], Sam Moore[1], Sami W. Rifai[3], Jhon del Aguila Pasquel[4], Alejandro Araujo Murakami[5], Renata Freitag[6], Alexandra C. Morel[7], Sheleme Demissie[8], Christopher E. Doughty[9], Imma Oliveras[1]. Darcy F. Galiano Cabrera[2], Liliana Durand Baca[10], Filio Farfán Amézquita[2], Javier E. Silva Espejo[11], Antonio C.L. da Costa[12], Erick Oblitas Mendoza[13], Carlos Alberto Quesada[13], Fidele Evouna Ondo[14], Josué Edzang Ndong[14], Kathryn L. Jeffery[22], Vianet Mihindou[15], Lee J. T. White[15], Natacha N'ssi Bengone[15], Forzia Ibrahim[16], Shalom D. Addo-Danso[16], Akwasi Duah-Gyamfi[16], Gloria Djaney Djagbletey[16], Kennedy Owusu-Afriyie[16], Lucy Amissah[16], Armel T. Mbou[17], Toby R. Marthews[18], Daniel B. Metcalfe[19], Luiz E.O. Aragão[20], Ben H. Marimon-Junior[6], Beatriz S. Marimon[6], Noreen Majalap[21], Stephen Adu-Bredu[16], Katharine A. Abernethy[22], Miles Silman[23], Robert M. Ewers[24], Patrick Meir[25,26], and Yadvinder Malhi[1]

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Affiliations:

* Author for correspondence: **Walter Huaraca Huasco (stwamayr@gmail.com)**

[1](Huaraca Huasco; Riutta; Girardin; Moore; Oliveras; Malhi) Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

[2](Puma Vilca; Hancco Pacha; Farfán Amézquita; Galiano Cabrera) Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú

[3](Rifai) ARC Centre of Excellence for Climate Extremes, University of New South Wales, Sydney, NSW 2052, Australia

[4](del Aguila Pasquel) Instituto de Investigaciones de la Amazonía Peruana (IIAP), Iquitos, Perú

[5](Araujo Murakami) Museo de Historia Natural Noel Kempff Mercado Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565 Casilla Postal 2489, Santa Cruz, Santa Cruz, Bolivia

[6](Freitag, Marimon, Marimon-Junior) Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, CEP 78690-000, Nova Xavantina, MT, Brazil

[7](Morel) Department of Geography and Environmental Science, University of Dundee, Dundee, DD1 4HN, UK

[8](Demissie) Water and Land Resources Centre of Addis Ababa University, Ethiopia

[9](Doughty) School of Informatics, Computing and Cyber systems, Northern Arizona University, Flagstaff, AZ 860011-5640 USA
[10](Durand Baca) Universidad Nacional Federico Villarreal de Lima, Lima, Perú
[11](Silva-Espejo) Departamento de Biología, Universidad de La Serena, La Serena, Chile
[12](ACL da Costa) Instituto de Geosciências, Universidade Federal do Pará, Belém, Brazil
[13](Quesada, Oblitas Mendoza) Instituto Nacional de Pesquisas da Amazônia, Manaus, Cx. Postal 2223-CEP 69080-971, Brazil
[14](Evouna Ondo, Edzang Ndong) Agence Nationale des Parcs Nationaux, Libreville, Gabon
[15](Mihindou, White, Bengone) Ministère de la Foret, de la Mer, de l'Environnement, Chargé Du Plan Climat, Libreville, Gabon.
[16](Ibrahim, Addo-Danso, Duah-Gyamfi, Djagbletey, Owusu-Afriyie, Amissah, Adu-Bredu) Forestry Research Institute of Ghana, Council for Scientific and Industrial Research, University P.O. Box 63, Kumasi, Ghana.
[17](Mbou) Centro Euro-Mediterraneo sui Cambiamenti Climatici, Via Augusto Imperatore 16, 73100 Leece, Italy.
[18](Marthews) UK Centre for Ecology & Hydrology (UKCEH), Wallingford OX10 8BB, UK
[19](Metcalfe) Physical Geography and Ecosystem Science, Lund University, Lund, Sweden
[20](Aragão) Divisão de Sensoriamento Remoto-DIDSR, Instituto Nacional de Pesquisas Espaciais, São Jose dos Campos, São Paulo, Brazil
[21](Majalap) Sabah Forestry Department, Forest Research Centre, Sandakan, Sabah, Malaysia
[22](Abernethy, Jeffery) Faculty of Natural Sciences, University of Stirling, UK
[23](Silman) Department of Biology, Wake Forest University, Winston-Salem, NC 27106, USA
[24](Ewers) Department of Life Science, Imperial College London, Ascot, UK
[25](Meir) Research School of Biology, Australian National University, ACT 2602 Australia
[26](Meir) School of Geosciences, University of Edinburgh, Crew Building, Kings Buildings, Edinburgh EH9 3FF, United Kingdom

Abstract

Fine roots constitute a significant component of the net primary productivity (NPP) of forest ecosystems but are much less studied than above-ground NPP. Comparisons across sites and regions are also hampered by inconsistent methodologies, especially in tropical areas. Here, we present a novel dataset of fine root biomass, productivity, residence time, and allocation in tropical old-growth rainforest sites worldwide, measured using consistent methods, and examine how these variables are related to consistently determined soil and climatic characteristics. Our pantropical dataset spans intensive monitoring plots in lowland (wet, semi-deciduous, deciduous) and montane tropical forests in South America, Africa, and Southeast Asia (n=47). Large spatial variation in fine root dynamics was observed across montane and lowland forest types. In lowland forests, we found a strong positive linear relationship between fine root productivity and sand content, this relationship was even stronger when we considered the fractional allocation of total NPP to fine roots, demonstrating that understanding allocation adds explanatory power to understanding fine root productivity and total NPP. Fine root residence time was a function of multiple factors: soil sand content, soil pH, and maximum water deficit, with longest residence times in acidic, sandy, and water-stressed soils. In tropical montane forests, on the other hand, a different set of relationships prevailed, highlighting the very different nature of montane and lowland forest biomes. Root productivity was a strong positive linear function of mean annual temperature, root residence time was a strong positive function of soil nitrogen content in montane forests, and lastly decreasing soil P content increased allocation of productivity to fine roots. In contrast to the lowlands, environmental conditions were a better predictor for fine root productivity than for fractional allocation of total NPP to fine roots, suggesting that root productivity is a particularly strong driver of NPP allocation in tropical mountain regions.

Keywords: Fine roots, biomass, productivity, residence time, allocation, turnover, soil

4.1 Introduction

Fine root biomass, productivity, and residence time are key factors in shaping both ecosystem productivity and below-ground carbon dynamics. Compared to above-ground biomass stock and productivity, fine root dynamics and their controlling factors remain poorly understood, especially in tropical forest ecosystems. Previous studies show that fine root dynamics across global forest ecosystems vary: fine root biomass and productivity are higher in tropical forests than temperate and boreal forests (Finér et al., 2011; Wang et al., 2018) and residence time increases from tropical regions towards boreal forests (Finér et al., 2011; Gill and Jackson, 2000). Across old-growth Amazon forests, soil organic carbon content down to 30 cm is negatively related to soil nutrient content and fine root biomass is the largest contributor to the soil organic carbon pool in the nutrient poor soils (Quesada et al., 2020).

Fine roots (here defined as roots under 2 mm diameter) are the critical pathway for water and nutrient uptake, and organic carbon transport, and also act in symbiosis with fungi for uptake processes (Jackson et al., 1997; McCormack et al., 2014). Fine root biomass has been quantified in several studies for high and low soil nutrient conditions across tropical forests, using soil cores of varying diameters. In tropical lowland forest, fine root biomass increases with soil sand content (Barbosa et al., 2012; Jiménez et al., 2009; Kochsiek et al., 2013; Priess et al., 1999; Silver et al., 2000) and with precipitation at regional scale (Green et al., 2005; Ibrahim et al., 2020). Fine root biomass increases with elevation (Girardin et al., 2013; Kitayama & Aiba, 2002; Leuschner et al., 2007; Moser et al., 2010; Okada et al., 2017; Sierra Cornejo et al., 2020) in tropical forests. Fine root biomass has also been shown to increase with decreasing mean annual temperature, soil pH, and C:N ratio in Ecuadorian montane forests (Moser et al., 2010) and with decreasing mean annual temperature and soil P availability in Bornean montane forests (Okada et al., 2017).

There are far fewer measurements of fine root productivity and dynamics because such measurements require frequent return visits to field sites, which may be time consuming and laborious. Net primary productivity of fine roots is defined as the new fine root biomass under 2 mm diameter accumulated per unit ground surface area per unit time. The most common technique used to quantify fine root net primary productivity is the ingrowth core mesh (Addo-Danso et al., 2016; Marthews et al., 2014; Metcalfe et al., 2007; Vogt et al., 1998). To date, high variability of fine root productivity has been recorded for different tropical forest types, which is driven by soil properties and climatic variables (Aragão et al., 2009; Kho et al., 2013; Metcalfe et al., 2008; Moore et al., 2018; Riutta et al., 2018; Violita et al., 2016), which is driven by soil properties and climatic variables. In lowland Amazon forest, fine root productivity is influenced by soil texture (Jiménez et al., 2009; Silver et al., 2005). In montane forests, the response of fine root productivity to abiotic drivers has not shown consistent patterns across sites. In Ecuador, fine root productivity increased with decreasing temperature and increasing rainfall, elevation, and soil C:N ratio (Moser et al., 2011; Röderstein et al., 2005). However, in the Peruvian Andes, fine root productivity was high at cloud base zone, and fine root productivity increased with increasing temperature (Girardin et al., 2013). In Bornean montane forests, fine root productivity was reported to increase with increasing temperature and soil phosphorus, but decreased with increasing soil N (Okada et al., 2017).

Fine root residence time refers to how long any unit of biomass remains within the living structures of fine roots tissues, and it represents a proxy for mean fine root lifetime, weighted by root biomass, and is thereby a key determinant of soil carbon accumulation and nutrient availability from root mortality (Castanho et al., 2013; Majdi et al., 2005; Strand et al., 2008). Root residence time decreases with high root mortality, and it is the inverse of root turnover rate (Assefa et al., 2017; Friend et al., 2014; Osawa et al., 2012; Sierra Cornejo et al., 2020). Lifetime of fine roots has been reported to decrease with soil fertility in lowland

Amazonian forests (Aragão et al., 2009) and in response to N soil addition (Peng et al., 2017). Several factors can contribute to increased root residence time, including root thickness as an anti-herbivore defence, water limitation, and low nutrient availability (Silver et al., 2005). In tropical montane forests, temperature has been reported to be the main driver of fine root residence time (Girardin et al., 2013; Graefe et al., 2008a, 2008b; Okada et al., 2017).

Most studies on fine root productivity do not measure above-ground productivity, and consequently, the fractional allocation to fine roots: hence it is not clear how much inter-site variation in root productivity is caused by variation in total net primary productivity (NPP), or by variation in the proportion of NPP that is allocated to the fine root biomass production. However, the fractional allocation of NPP to fine roots rather than the absolute fine root productivity itself may be the component which is best predicted from environmental conditions, because allocation reflects the overall strategy of the trees, such as trade-offs between investment in leaves, woody tissues, and fine roots. On the other hand, if fine roots are prioritised and less involved in the trade-offs, environmental would predict root productivity better that predicted allocation to roots (Malhi et al., 2011). Soil nutrient limitation plays a key role in controlling the fractional allocation of total NPP to fine roots, with increasing allocation to fine roots on lower fertility sites and highly weathered soils (Doughty et al., 2018; Wright et al., 2011; Yavitt et al., 2011). Highly-weathered lowland tropical soils are often old and associated with low pH, high concentrations of aluminium (Al), iron (Fe) oxides, and with P often being a key limiting nutrient (Laliberté et al., 2015). Fractional allocation of total NPP to fine roots is crucial for understanding how ecosystems will respond to soil disturbance and climatic variables (Green et al., 2005; Yuan & Chen, 2010).

This is one of the first analysis to date of a global tropical fine root dataset, and the first to use the exact same protocol across sites; most studies of fine root dynamics in the tropics tend to focus on a particular site or biogeographic region (e.g. Girardin et al., 2013; Okada et

al., 2017; Sierra Cornejo et al., 2020), or synthesise results across studies that employ different methodologies (Moser et al., 2010; Röderstein et al., 2005). Hence it remains unclear whether trends found in any one region are universal features of tropical forest biomes. Here, we collected and analysed a unique dataset for fine root biomass carbon stock, productivity, residence time, and fractional allocation of total NPP to fine roots from wet, semi-deciduous, deciduous, and montane old-growth forest types that span tropical regions in South America, Africa, and Southeast Asia. This global dataset is unique because (1) root dynamics data were collected to a standardised protocol across all sites; (2) soil data from all regions and sites were collected and analysed to a standardised laboratory protocol, enabling reliable cross-site comparison of the importance of soil factors; and (3) the root measurements are coupled with measurements of above-ground NPP, enabling proportional allocation to fine roots to be quantified. With these data, we address the following questions:

(Q1) How does fine root biomass, productivity, residence time, and fractional allocation of total NPP to fine roots vary across tropical forests?

(Q2) Are there consistent patterns in how climatic variables and physical and chemical soil properties drive fine root dynamics in tropical forests at the global scale?

4.2 Materials and methods

4.2.1 Study sites

We collected root dynamics data in 47 plots in 22 sites across three continents in lowland and montane tropical forests. These one-hectare plots are part of the Global Ecosystem Monitoring network (GEM, Malhi et al., 2021), which uses standardise measurement protocols across all sites. The lowland forests sites are located in Bolivia, Brazil, Gabon, Ghana, Malaysia, and Peru (Table 4.1, Figure 4.1). They span a rainfall gradient from 1310 and 3154 mm yr^{-1}, and were classified into wet tropical forests (WTF), semi-deciduous tropical forests (SDTF), and deciduous tropical forests (DTF) based on their seasonal patterns in rainfall (Feng et al., 2013;

Rifai et al., 2018). The montane tropical forests (MTF) study sites are located across an elevation gradient that ranges between 595 and 3537 m asl in Peru and Ethiopia (Table 4.1).

In Peru, the lowland plots (n = 7) are located in Tambopata National Reserve (TAM), Allpahuayo-Mishana National Reserve (ALP), Manu National Park, and Jenaro Herrera Local Conservation Area (JEN), and the montane plots (n=12) are located in or adjacent to Manu National Park. The Peruvian plots are part of Amazon Forest Inventory Network (RAINFOR), Andes Biodiversity and Ecosystem Research Group (ABERG), GEM, and Instituto de Investigaciones de la Amazonia Peruana (IIAP) projects (del Aguila-Pasquel et al., 2014; Malhi et al., 2017).

In Bolivia, the two plots are located in semi-deciduous tropical forests of private properties at the Hacienda Kenia (KEN) in Guarayos Province, Santa Cruz (Araujo-Murakami et al., 2014). In the Brazilian Amazon, two plots are located in WTF of Caxiuanã National Forest Reserve (CAX), Pará, eastern Brazilian Amazon (da Costa et al., 2014), two in the privately owned Fazenda Tanguro of Mato Grosso State (TAN), dry forest near the southern boundary of the Amazon rainforest (Rocha et al., 2014), and two in Nova Xavantina (NXV), cerrado and cerradão transitional forest near the Bacaba Municipality Reserve, Nova Xavantina (Gvozdevaite et al., 2018).

In Ghana, three evergreen plots are located in the Ankasa Conservation Area (ANK), two semi-deciduous plots are located in the Bobiri Forest Reserve (BOB), and five plots are located in dry forest and mesic savanna in the Kogyae Strict Nature Reserve (KOG) (Moore et al., 2018). In Gabon, two plots are located in Ivindo National Park (IVI), and two plots are located in Lopé National Park (LPG) (Rifai et al., 2018). In Ethiopia, two plots are located at transitional montane rainforest of Yayu Forest Coffee Biosphere Reserve (YAY), as part of the Exploring the Ecosystems Limits to Poverty Alleviation in African forest-agriculture Landscapes (ECOLIMITS) project (Morel et al., 2019).

In Sabah, Malaysian Borneo, two plots are located in the Maliau Basin Conservation Area (MLA) and two in the Danum Valley Conservation Area (DAN). These plots are part of intensive monitoring of the Stability of Altered Forest Ecosystem (SAFE) programme (Ewers et al., 2011; Riutta et al., 2018). The Danum plots are within the 50 ha CTFS-ForestGEO monitoring plot.

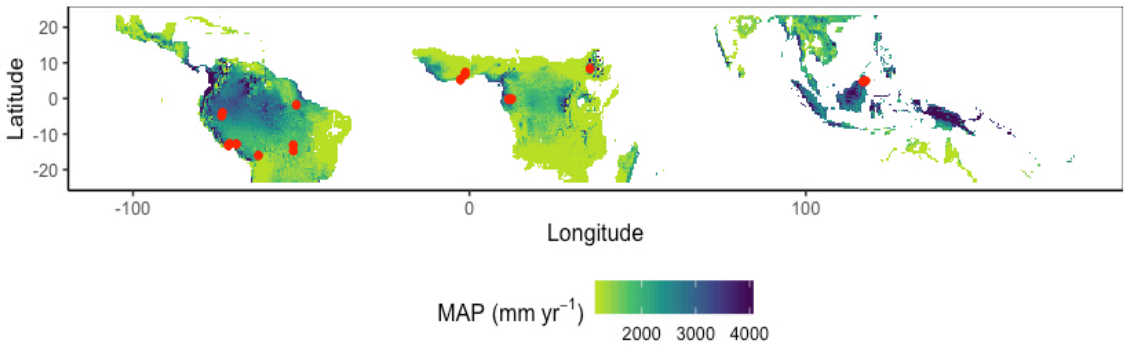


Figure 4.1. The Global Ecosystem Monitoring Network (GEM) permanent plot locations across forest types of wet, semi-deciduous, deciduous, and montane tropical forests. Colours indicate mean annual precipitation (MAP) and red dots show the study sites.

4.2.2 Measurements of fine root dynamics

Total fine root biomass carbon stock ($Cstock_{fr}$) was recorded from four (YAY-17, YAY-55), nine (ANK-01, ANK-02, ANK-03, TRU-03, TRU-07, TRU-08, and TON-01), or sixteen (all other sites) soil cores per plot. A post hole digger shovel was used to collect soil cores with a diameter of 12 cm and depth of 30 cm from which all roots were extracted. The coring holes and the newly root-free soil were then used for installing root ingrowth cores. The cylindrical ingrowth cores of 12 cm diameter and 40 cm length were made of plastic wire mesh of 1.5 cm space cloth, which allowed the regrowth of roots and the movement of soil macrofauna into the core. The ingrowth cores were installed into the holes down to 30 cm depth, with the top 10 cm of the core sticking out of the soil. Each core was filled with its native soil and the soil

vertical profile and bulk density maintained as natural as possible. The cores were harvested every three months to quantify *fine root productivity* (NPP_{fr}) and reinstalled again in the same hole. Roots were manually collected from the cores, following the GEM protocol (Marthews et al., 2014; Metcalfe et al., 2007). Fine roots in each core were extracted for a period of 40 min (4 x10 min) and the total root mass in the sample was estimated from a cumulative root mass over time curve, up to 120 min (Girardin et al., 2013). The 40-minute fine root technique extraction has been used for fine root dynamic studies in Africa (Moore et al., 2018), Southeast Asia (Kho et al., 2013, Riutta et al., 2018), and Amazon basin (Aragão et al., 2009; Girardin et al., 2013; Metcalfe et al., 2008). This process allows the roots search period to have a reasonable time limit in the field while considering that a small fraction of the fine roots is likely to remain uncollected (Metcalfe et al., 2007; Riutta et al., 2018). Collected roots were cleaned using water and fine sieves to avoid loss of fine roots during the rinsing process, and were oven dried at 70 ^{o}C until constant mass. Fine roots ($\leq$ 2 mm diameter) were separated and weighed to determine the total fine root C stock (Aragão et al., 2009; Metcalfe et al., 2008). To assess fine root C stock (Mg C ha^{-1}) and productivity (Mg C ha^{-1} yr^{-1}), dry mass was converted into carbon units by assuming a carbon content of 45%. We mined the Fine-Root Ecology Database (FRED; roots.ornl.gov; Iversen et al., 2017) and calculated the average fine root carbon content of broadleaved species, 45% with standard error of 0.12%, n = 1771. To be consistent with other studies within the GEM network (Malhi et al. 2021 and references therein), we express fine root stock and productivity in units of carbon, rather than dry mass. We estimated the fine root C stock and productivity down to 30 cm soil depth in all plots.

Fine root carbon residence time (RT_{fr}) was calculated dividing the average $Cstock_{fr}$ by annual NPP_{fr} (Girardin et al., 2010). *Fractional allocation of total NPP to fine root productivity* ($Allocation_{fr}$) was assessed by dividing the NPP_{fr} recorded in this study by total ecosystem net primary productivity (NPP_{total}) measured in each plot in previous studies (Araujo-Murakami et

al., 2014; del Aguila-Pasquel et al., 2014; Girardin et al., 2014; Huaraca Huasco et al., 2014; Malhi et al., 2017; Moore et al., 2018; Riutta et al., 2018). NPP_{total} was the sum of canopy productivity (estimated from canopy litterfall), wood productivity (stem and coarse wood productivity of stems ≥10 cm diameter at breast height, based on allometric equations), and fine root productivity.

4.2.3 Soil properties and climatic variables

Soils data (Table 4.1) were collected from all sites to a consistent RAINFOR protocol (Quesada et al., 2009) and analysed to a common and cross-calibrated protocol either at the INPA soil laboratory in Manaus, Brazil (for samples from Brazil, Bolivia, and Peru sites) or at the University of Leeds (samples from all other sites). Mean annual precipitation (MAP) and temperature (MAT) were calculated using data from automatic weather stations installed close to each plot (Table 4.1). The mean maximum cumulative water deficit (MCWD) was calculated from precipitation data as the peak of dry season water deficit during the root sampling period, following Aragão et al. (2007), assuming an invariant evapotranspiration rate of 1200 mm $year^{-1}$.

Table 4.1. Characteristics of the Global Ecosystem Monitoring Network 1ha permanent plots across forest types of wet tropical forests (WTF), semi-deciduous tropical forests (SDTF), deciduous tropical forests (DTF), and montane tropical forests (MTF): elevation (Elev, m asl), latitude (Lat., decimal degrees), longitude (Long., decimal degrees), mean annual precipitation (MAP, mm yr^{-1}), mean annual temperature (MAT, ^{o}C), potential of hydrogen (pH, H_2O), maximum cumulative water deficit (MCWD, mm yr^{-1}), and soil properties of soil sand, clay, and silt percentage content (%), total nitrogen (N, %), total carbon-nitrogen ratio (C:N), total phosphorus (P, mg kg^{-1}), total aluminium (Al, mg kg^{-1}), calcium (Ca, mg kg^{-1}), total potassium (K, mg kg^{-1}), total magnesium (Mg, mg kg^{-1}), total sodium (Na, mg kg^{-1}), and soil cation exchange capacity (CEC, mmol+kg^{-1}).

Country	Site	Plot code	Forest type	Soil type	Elev. (m asl)	Obs. period	Lat.	Long.	MAP	MAT	MCWD	Sand	Silt	Clay	pH	N	C: N	P	Al	Ca	K	Mg	Na	CEC
Bolivia	Kenia	KEN-01	SDTF	Cambisols	384	2009-2017	-16.02	-62.73	1310	24.2	-273.52	58.05	22.82	19.13	NA	0.22	10.91	447.1	3.1	1291	126.6	94.6	0.7	75.9
		KEN-02	SDTF	Cambisols	384	2009-2017	-16.01	-62.74	1310	24.2	-273.52	55.48	26.27	18.25	NA	0.17	11.76		10.3	955.2	84.4	131.5	0.8	61.9
Brazil	Caxiuana	CAX-04	WTF	Acrisols	47	2009-2016	-1.86	-51.44	2311	25	-463.73	83.7	5.6	10.7	NA	0.1	13.8	37.4	10.3	1.2	1.2	0.9	0.8	1.3
		CAX-06	WTF	Acrisols	47	2009-2011	-1.72	-51.46	2311	25	-463.73	32.5	13.7	53.8	NA	0.1	12.9	178.5	168.8	25.7	18.5	17.9	19.1	22.8
	Nova	NXV-01	DTF	Ferrasols	312	2014-2016	-14.7	-52.35	1530	25.2	-387.31	85.5	3.4	11.1	NA	0.1	NA	107.5	NA	19.5	39.9	7.6	NA	12
	Xavantina	NXV-02	DTF	Ferrasols	324	2014-2016	-14.71	-52.35	1530	25.2	-387.31	75.3	6.9	17.8	NA	0.1	NA	129.5	NA	50	46.5	27.5	NA	18.1
	Tanguro	TAN-01	SDTF	Ferrasols	385	2009-2011	-13.08	-52.39	1740	25	-412.81	45.7	5.4	48.9	NA	0.2	15.9	147	154.4	9	33.7	8.1	7.7	19.5
		TAN-02	SDTF	Ferrasols	385	2009-2011	-13.08	-52.39	1740	25	-412.81	45.7	5.4	48.9	NA	0.2	15.9	147	154.4	9	33.9	8.2	7.8	19.5
Peru	Alpahuayo	ALP-11	WTF	Gleysol	120	2010-2011	-3.95	-73.43	2689	26.6	-29.93	65	20	15	NA	0.1	11.9	110	249.8	20	29.3	9.8	2.3	30.4
		ALP-12	WTF	Arenosol	150	2010-2011	-3.95	-73.43	2689	26.6	-29.93	82	16	2	NA	0.08	14.13	38	5.4	52	23.4	12.2	0	4.8
	Jenaro	JEN-11	WTF	Acrisols	131	2014-2015	-4.88	-73.63	3100	25.2	-26.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Herrera	JEN-12	WTF	Podzols	135	2014-2016	-4.9	-73.63	3100	25.2	-26.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Tambopata	TAM-05	WTF	Cambisols	223	2006-2017	-12.83	-69.27	2545	24.4	-165.55	40	17	44	NA	0.16	9.44	256.3	382.5	6	35.1	12.2	2.3	44.8
		TAM-06	WTF	Alisols	215	2006-2017	-12.84	-69.3	2545	24.4	-165.55	2	52	46	NA	0.17	7.06	528.8	60.3	536	58.5	263.5	4.6	56.8
		TAM-09	WTF	Alisols	219	2006-2017	-12.83	-69.27	2545	24.4	-165.55	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Pantiacolla	PAN-02	MTF	Cambisols	595	2013-2014	-12.65	-71.26	2366	23.5	-33.78	17.65	37.95	44.4	NA	0.34	10.6	709	231.65	5.18	16.65	5.51	NA	NA
		PAN-03	MTF	Plinthosol	848	2013-2014	-12.64	-71.27	2835	21.9	-33.78	44.95	22.65	32.4	NA	0.22	11.3	1174.8	129.28	8.52	14.43	7.68	NA	NA
	Tono	TON-01	MTF	Cambisols	1000	2007-2008	-12.96	-71.57	3087	20.7	NA	27.83	32.42	39.75	3.84	0.42	12.22	751	NA	79.2	154.26	97.12	11.91	23.96
	San	SPD-02	MTF	Cambisols	1527	2009-2013	-13.05	-71.54	5302	18.8	-0.16	37.51	17.79	44.71	3.75	0.88	14.93	1630.71	683.11	183.21	154.36	317.28	28.26	42.21
	Pedro	SPD-01	MTF	Cambisols	1776	2009-2013	-13.05	-71.54	5302	17.4	-0.16	31.35	26.97	41.68	3.65	1.19	18.01	1071.14	460.43	74.35	41.79	324.28	20	32.32
	Trocha	TRU-08	MTF	Cambisols	1885	2007-2008	-13.07	-71.56	2472	18	NA	70.01	20.99	9	3.93	1.23	21.17	562.83	NA	75.42	95.9	38.68	26.09	45.47
	Union	TRU-07	MTF	Cambisols	2020	2007-2008	-13.07	-71.56	1827	17.4	NA	57.21	26.29	16.5	4.03	0.81	17.79	495.97	NA	78.91	64.1	79.01	57.83	39.84
		TRU-04	MTF	Umbrisol	2758	2013-2014	-13.11	-71.59	2318	13.5	-0.16	13.61	12.5	73.89	3.23	1.99	15.47	746.76	383.96	70.93	182.31	87.24	43.48	37.75
		TRU-03	MTF	Umbrisol	3044	2007-2008	-13.11	-71.6	1776	11.8	NA	0	0	0	3.93	1.55	16.76	787.31	NA	68.93	246.41	71.6	39.13	36.07
	Esperanza	ESP-01	MTF	Umbrisol	2863	2009-2016	-13.18	-71.59	1560	13.1	-0.33	1.37	40	58.63	4.17	1.48	18.82	980.82	430.9	62.38	238.1	87.9	42.52	35.25
	Wayqecha	WAY-01	MTF	Umbrisol	3045	2009-2016	-13.19	-71.59	1560	11.8	-0.33	43.65	16.5	39.85	4	0.88	21.23	1413.59	469.07	66.57	222.26	154.07	26.17	42.54
	Acjanaco	ACJ-01	MTF	Umbrisol	3537	2013-2014	-13.15	-71.63	1980	9	-1.17	4.13	56.77	39.1	NA	0.94	12.83	586.93	268.07	10.83	23.52	10.07	NA	NA

Country	Site	Plot code	Forest type	Soil type	Elev. (m asl)	Obs. period	Lat.	Long.	MAP	MAT	MCWD	Sand	Silt	Clay	pH	N	C: N	P	Al	Ca	K	Mg	Na	CEC
Ethiopia	Yayu	YAY-17	MTF	NA	1500	2015-2017	8.39	35.8	2100	26.1	-264.03	62.54	22.8	14.65	6.28	0.35	11.6	989.52	0.09	824.91	79.86	244.62	2.7	63.46
		YAY-55	MTF	NA	1327	2015-2017	8.37	35.8	2100	26.1	-245.73	36.24	27.78	35.98	6.5	0.38	12.97	1310.87	0.23	819.18	231.82	188.13	1.86	62.39
Gabon	Ivindo	IVI-01	SDTF	Cambisols	578	2013-2015	-0.17	12.53	1738	23.5	-80.46	59.5	7.4	33.1	3.8	0.1	12.4	286.9	243.4	6.2	25	8	1.1	28.7
		IVI-02	SDTF	Cambisols	458	2013-2015	-0.13	12.54	1738	23.5	-80.46	46	9.6	44.4	3.6	0.2	11.7	770.9	178	21	27.4	10	0.6	22.4
	Lopé	LPG-01	SDTF	Ferrasols	406	2013-2015	-0.17	11.57	1263	25.6	-106.13	19.3	36	44.7	3.8	0.1	10.6	130.7	277	5.4	18.3	5.3	1.8	32
		LPG-02	SDTF	Ferrasols	302	2013-2015	-0.22	11.62	1263	25.6	-106.13	55.3	11.5	33.2	4.1	0.1	12.3	64.7	125.6	28.2	60.4	21	1.2	18.7
Ghana	Kogaye	KOG-02	DTF	Nitisols	229	2013-2016	7.26	-1.15	1313	26.5	-160.52	82.41	15.34	2.26	6.4	0.05	10.18	60.28	0.2	242.4	35.6	75.9	0.3	19.3
		KOG-03	DTF	Arenosol	229	2014-2016	7.26	-1.15	1313	26.5	-160.52	82.41	15.34	2.26	6.4	0.05	10.18	60.28	0.2	242.4	35.6	75.9	0.3	19.3
		KOG-04	DTF	Arenosol	197	2013-2016	7.3	-1.18	1313	26.5	-160.52	79.68	17.02	3.3	6.25	0.04	12.21	65.97	1	209.7	27.8	69.6	0.6	17
		KOG-05	DTF	NA	221	2013-2016	7.3	-1.16	1313	26.5	-160.52	76.95	18.71	4.34	6.09	0.03	14.25	71.65	1.8	177	19.9	63.3	0.9	14.8
		KOG-06	DTF	NA	221	2014-2016	7.3	-1.16	1313	26.5	-160.52	76.95	18.71	4.34	6.09	0.03	14.25	71.65	1.8	177	19.9	63.3	0.9	14.8
	Ankasa	ANK-01	WTF	Oxisols	114	2012-2017	5.27	-2.69	2050	26.7	-79.33	63.1	15.3	21.6	4.7	0.1	12.8	126	164.4	6.5	17.8	19.1	7.4	20.9
		ANK-02	WTF	Oxisols	114	2012-2017	5.27	-2.7	2050	26.7	-79.33	63.1	15.3	21.6	4.7	0.1	12.8	126	164.4	6.5	17.8	19.1	7.4	20.9
		ANK-03	WTF	Oxisols	78	2012-2017	5.27	-2.69	2050	26.7	-79.33	75.9	11.4	12.8	4.8	0.1	12.7	88.2	126.7	33.7	22.2	27.6	6.2	18.9
	Bobiri	BOB-01	SDTF	Ultisols	235	2013-2016	6.7	-1.32	1345	26.1	-204.78	55.47	26.8	17.7	6.7	0.1	9.4	210.4	1.4	620.1	54.8	127.5	0.9	46
		BOB-02	SDTF	Ultisols	235	2013-2017	6.75	-1.34	1345	26.1	-204.78	46.75	24.5	28.8	7.9	0.2	11.8	320	2	948.4	29.2	164.7	0.9	46
Malaysia	Danum	DAN-04	WTF	Orthic	225	2015-2017	4.95	117.8	2977	26.5	-31.07	36.53	40.94	22.52	5.55	0.11	9.15	447.01	3.22	590.2	20.58	398.25	24.73	64.18
	Valley	DAN-05	WTF	Acrisols	235	2015-2017	4.95	117.79	2977	26.5	-31.07	34.14	42.02	23.84	4.51	0.13	8.06	217.59	253.27	87.62	68.7	165.1	6.22	48.12
	Maliau	MLA-01	WTF	Podzols	318	2012-2017	4.75	116.97	3154	25.7	-29.01	43.5	33.9	22.6	4.2	0.1	5.5	171.7	436.4	15.3	62.9	45.5	1.8	36.4
	Basin	MLA-02	WTF	Podzols	326	2012-2017	4.75	116.95	3154	25.7	-29.01	19	57.9	23.1	4.4	0.1	6.4	74.2	186.1	205.1	59.6	214.2	15.4	43.2

4.2.4 Statistical analyses

To examine the drivers of fine root dynamics across the 47 plots, we applied generalised additive models (GAMs) separately for lowland and montane forests, with soil properties and climatic variables as explanatory factors, using *mgcv* package for R (Wood, 2011). First, to reduce dimensionality and to identify the most orthogonal soil properties, we conducted a principal component analysis (PCA) of soil variables for lowland and montane forests with the measurements of total concentration of soil texture (sand, silt, and clay), pH, nitrogen (N), carbon-nitrogen ratio (C:N), phosphorus (P), aluminium (Al), calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), and soil cation exchange capacity (CEC). The PCA analysis was conducted with the *factoextra* package for R (Kassambara & Mundt, 2020) and the variables with the highest loadings on the first four PCA axes were selected as potential explanatory variables in the regression models for fine root dynamics. Soil sand content (%), pH, P, and K were selected for lowland forest, and P, N, soil clay content (%), and K for montane forests (Table S4.1 and Figure S4.1). In addition, the available climatic variables MAP, MCWD, and MAT were selected as potential explanatory variables for multiple regression for lowland and montane forests.

The analyses were carried out with multiple regression models, to understand which combination of explanatory variables best explained each fine root dynamics component ($Cstock_{fr}$, NPP_{fr}, RT_{fr}, and $Allocation_{fr}$). $Cstock_{fr}$, NPP_{fr}, and RT_{fr} were modelled using Gamma distribution (values are positive, variance increases with increasing mean) with a log link function. $Allocation_{fr}$ was modelled with the Beta distribution and logit link function ($Allocation_{fr}$ is always greater than 0 and less than 1).

Akaike's information criterion (AICc) for small samples ($n < 40$) was used to compare the models, the minimum AICc was selected as the best-fit estimator, and the models were

examined by *MuMIn* package (Bartón, 2020). All statistical analyses were conducted with R statistical software, version 3.6.0.

4.3 Results

4.3.1 Fine root biomass carbon ($Cstock_{fr}$)

High variability in fine root C stock was recorded across the lowland forest types of wet, semi-deciduous, and deciduous (Figure 4.2a), and along the montane tropical forest ecosystems (Figure 4.2b). The highest fine root C stock was recorded for a wet eastern Amazonian forest (CAX-06), and the lowest C stock was recorded for a wet Malaysian Bornean rainforest (DAN-04). Across the lowland forests the total fine root C stock varied by more than an order of magnitude between 0.85 ± 0.13 Mg C ha^{-1} and 24.29 ± 3.84 Mg C ha^{-1}. In montane forests, high variation of fine root C stock was recorded with elevation that ranged between 2.10 ± 0.18 Mg C ha^{-1} (595 m asl) and 6.25 ± 0.94 Mg C ha^{-1} (2020 m asl). We estimated a total pantropical fine root C stock average of 5.57 ± 0.64 Mg C ha^{-1}.

$Cstock_{fr}$ was a good predictor of NPP_{fr} across lowland forests, but was not a good predictor of NPP_{fr} in montane forests (Figure 4.3). The GAM models revealed that $Cstock_{fr}$ in lowland forests was best explained by total K soil content (Figure 4.4a; Table 4.2). In montane forests, the best model for $Cstock_{fr}$ included soil clay content with positive and marginally significant effects of P and MCWD (Figure 4.4g, h, i; Table 4.2).

4.3.2 Fine root net primary productivity (NPP_{fr})

We recorded high variation in NPP_{fr} across the lowland forests (Figure 4.2c). Highest NPP_{fr} was reported on an Amazonian white sand soil forest (ALP-11), and the lowest NPP_{fr} was recorded for a Malaysian Bornean forest (MLA-02). The highest NPP_{fr} was recorded for a semi-deciduous West African forest (BOB-02) and the lowest average was recorded for a semi-deciduous Amazon forest (TAN-02). NPP_{fr} across the lowland forest types ranged between 0.64 ± 0.07 Mg C ha^{-1} yr^{-1} and 6.86 ± 0.56 Mg C ha^{-1} yr^{-1}. The mean annual average of NPP_{fr}

along the montane forests varied between 0.97 ± 0.27 Mg C ha^{-1} yr^{-1} and 3.18 ± 0.55 Mg C ha^{-1} yr^{-1} and tended to decrease with increasing elevation (Figure 4.2d). Highest NPP_{fr} estimates were recorded in an eastern African montane forest (1327 m asl) and the lowest on an Andean upper montane forest (3500 m asl). The total average of NPP_{fr} across the pantropical forest was 2.43 ± 0.23 Mg C ha^{-1} yr^{-1}.

In the multiple GAM models, lowland forest NPP_{fr} was best explained through a positive relationship to soil sand content only (Figure 4.4b; Table 4.2; Table 4.3). In montane forests, NPP_{fr} was best explained by MAT, with a positive relationship (Figure 4.4j; Table 4.2).

4.3.3 Fine root residence time (RT_{fr})

Residence time varied between six months (KEN-01) and seven years (CAX-06) across the lowland forest sites, and between nine months (595 m asl) and five years (2758 m asl) along the montane forests (Figure 4.2e, f). The highest and lowest fine root residence time was recorded in lowland wet and semi-deciduous forests of the Amazon region. Little variation of RT_{fr} was recorded on montane forests. Across the elevation gradient, RT_{fr} increased with increasing elevation and decreasing mean annual temperature. The lowest residence time was recorded in a montane forest and the highest average RT_{fr} was recorded in an upper montane forest of the Peruvian Andean transect. Figure 4.3 shows the linear relationship between fine root C stock and productivity across lowland and montane forest ecosystems, to illustrate how the variability in residence time is driven by its two components ($RT_{fr} = Cstock_{fr}/NPP_{fr}$). The high fine root residence time was associated with high root C stock across lowland and montane tropical forests, with a positive and significant relationship in lowland forests. The pantropical average of root residence time was 2.35 ± 0.22 years.

The relationship between environmental variables and residence time were less clear. We found that soil pH was closely associated with RT_{fr} in lowland forests, with RT_{fr} increasing in both more basic and more acidic soils. Soil sand content and MCWD also have some

explanatory power (Figure 4.4; Table 4.2). In montane forests, RT_{fr} was associated most with total soil N content (Figure 4.4k; Table 4.2).

4.3.4 Fractional NPP allocation to fine roots ($Allocation_{fr}$)

Fractional allocation of total NPP to fine roots varied between 5 ± 1% and 49 ± 5% across the lowland forests, and between 10 ± 1% and 37 ± 4% in montane forests (Figure 4.2g). The highest proportional root allocation was recorded for a wet Amazon lowland forest (ALP-11) and lowest for a Malaysian Bornean wet rainforest (MLA-02). In addition, root allocation tended to increase from cloud base zone to upper montane forest and then decreased on tree line forests (3537 m asl) and highest root allocation was recorded at 2020 m asl (Figure 4.2h). The pantropical average proportion of productivity allocated to fine roots was 21 ± 2%.

$Allocation_{fr}$ was a function of soil sandiness in lowland forests and GAM analysis revealed that fine root allocation was best explained by soil sand content with a positive relationship (Figure 4.4f; Table 4.2; Table 4.3). In montane forests, fine root allocation was best explained by soil P content (Figure 4.4l; Table 4.2; Table 4.3). One of the clearest results of this analysis is that $Allocation_{fr}$ of NPP to fine roots is associated with soil sand content in lowland forests. This strong relationship does not hold in montane forests plots, where NPP_{fr} is a function of mean annual temperature.

Table 4.2. Summary of generalised additive models (GAMs) for fine root carbon stock ($Cstock_{fr}$, Mg C ha^{-1}), productivity (NPP_{fr}, Mg C ha^{-1} yr^{-1}), residence time (RT_{fr}, yr), and fractional allocation of total net primary productivity to fine roots ($Allocation_{fr}$), with climatic variables of mean annual temperature (MAT, ºC), and soil properties of soil sand content (Sand, %), potassium (K, mg kg^{-1}), phosphorus (P, mg kg^{-1}), nitrogen (N, %), maximum cumulative water deficit (MCWD, mm yr^{-1}), and potential hydrogen (pH H_2O, %) as explanatory variables. Standard error (SE), deviance explained (DE), root mean square error (RMSE), significance of the model coefficients P values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1), and Akaike information criterion (AIC). The best model (lowest AIC) for each response variable is presented here, for full model, see Table S4.2).

Forest types	Response variables	Explanatory variables	Estimate	SE	*P*	*DE*	*RMSE*	*AIC*
Lowland forests (Wet, Semi-deciduous, Deciduous)	$Cstock_{fr}$	Intercept	2.425728	0.262749	***	24.70%	5.32107	156.773
		K (mg kg^{-1})	-0.01664	0.005657	**			
	NPP_{fr}	Intercept	0.159532	0.280278		27.40%	1.668431	108.548
		Sand (%)	0.015856	0.004654	**			
	RT_{fr}	Intercept	2.644315	0.545779	***	56.90%	0.6477272	52.4028
		Sand (%)	-0.014561	0.00597	*			
		PH H_2O (%)	-0.422804	0.133904	**			
		MCWD (mm)	-0.009831	0.002936	**			
	$Allocation_{nfr}$	Intercept	-2.47168	0.2895	***	50.60%	0.0916062	-57.6311
		Sand (%)	0.02263	0.00453	***			
Montane forests (MTF)	$Cstock_{fr}$	Intercept	0.0606716	0.5108584		54.30%	0.9018852	51.6039
		P (mg kg^{-1})	0.0004674	0.0002748				
		Clay (%)	0.0191156	0.0074311	*			
		MCWD (mm)	-0.0013453	0.001084				
	NPP_{fr}	Intercept	-0.36622	0.28799		50.60%	0.5563	26.9086
		MAT	0.05285	0.01552	**			
	RT_{fr}	Intercept	0.4211	0.2437		40.10%	0.9098165	48.7975
		N (%)	0.6272	0.2341	*			
	$Allocation_{fr}$	Intercept	-0.4573069	0.341369		38.20%	0.06978606	-22.8033
		P (mg kg^{-1})	-0.0009314	0.0003831	*			

Table 4.3. Linear regression models for fine root carbon stock ($Cstock_{fr}$, Mg C ha^{-1}), productivity (NPP_{fr}, Mg C ha^{-1} yr^{-1}), residence time (RT_{fr}, yr), and fractional allocation of total net primary productivity to fine roots ($Allocation_{fr}$), with climatic variables of mean annual temperature (MAT, ºC), and soil properties of soil sand content (Sand, %), potassium (K, mg kg^{-1}), phosphorus (P, mg kg^{-1}), and nitrogen (N, %) as explanatory variables. Standard error (SE).

Forest types	Response variables	Explanatory variables	Estimate	SE	*T-value*	P	R^2
Lowland forests (Wet, Semi-deciduous, Deciduous)	$Cstock_{fr}$	Intercept	10.270422	1.935823	5.305456	0.000015	0.14
		K (mg kg^{-1})	-0.097197	0.041679	-2.332028	0.027715	
	NPP_{fr}	Intercept	0.809491	0.864430	0.936445	0.357051	0.18
		Sand (%)	0.039080	0.014353	2.722848	0.011014	
	RT_{fr}	Intercept	3.476324	0.755731	4.599946	0.000097	0.10
		Sand (%)	-0.025037	0.012362	-2.025319	0.053215	
	$Allocation_{fr}$	Intercept	0.023466	0.048756	0.481301	0.634043	0.43
		Sand (%)	0.003863	0.000810	4.771527	0.000052	
Montane forests (MTF)	NPP_{fr}	Intercept	-0.105399	0.536073	-0.196613	0.847421	0.53
		MAT (ºC)	0.113993	0.028894	3.945215	0.001945	
	RT_{fr}	Intercept	1.096767	0.548030	2.001289	0.068500	0.49
		N (%)	1.928536	0.526337	3.664068	0.003242	
	$Allocation_{fr}$	Intercept	0.365703	0.064382	5.680221	0.000204	0.32
		P (mg kg^{-1})	-0.000165	0.000066	-2.484225	0.032308	

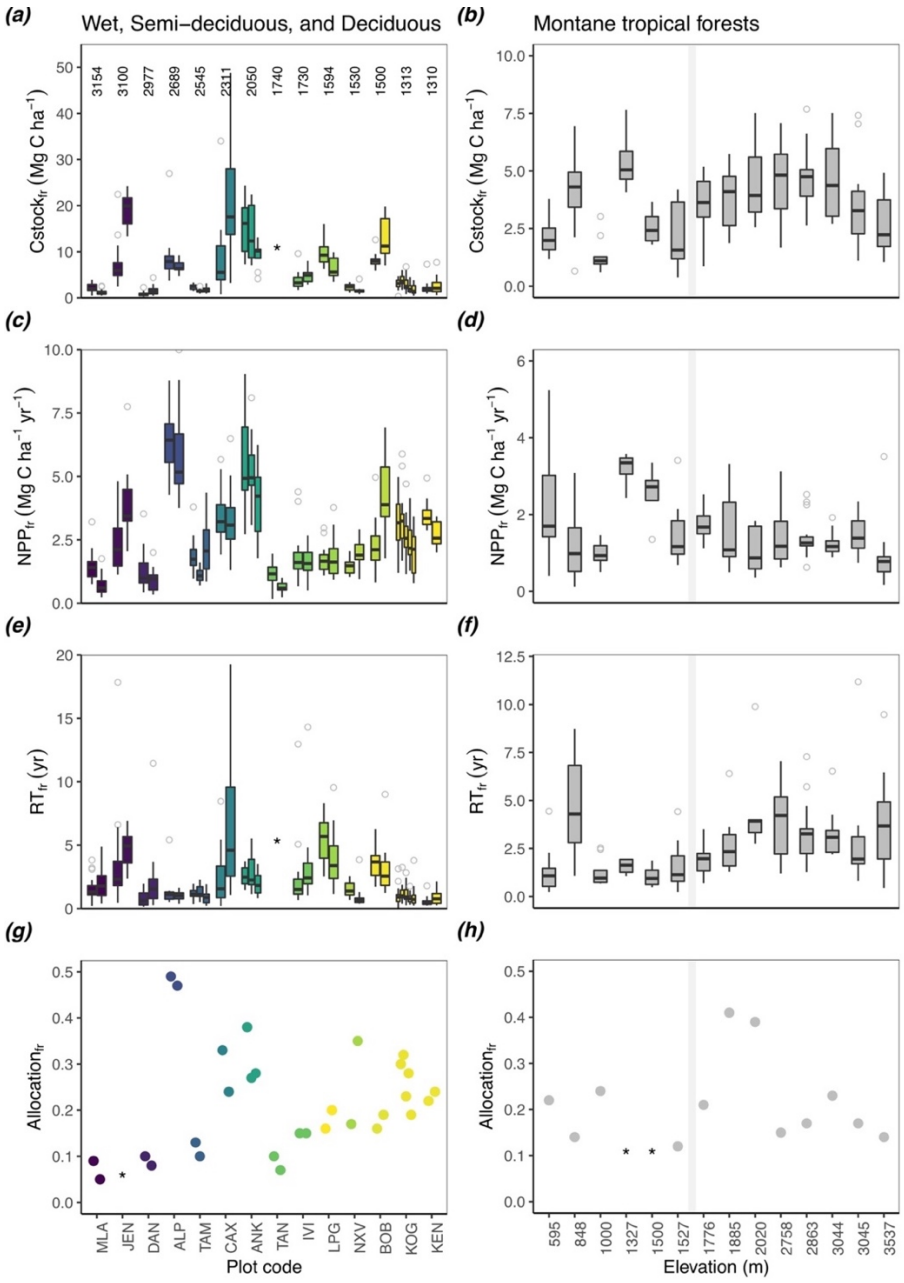


Figure 4.2. Variation in lowland (left) and montane (right) tropical forests of (a, b) total fine root carbon stock ($Cstock_{fr}$), (c, d) fine root productivity (NPP_{fr}), (e, f) fine root residence time (RT_{fr}), and (g, h) the fractional carbon allocation of total ecosystem NPP to fine roots ($Allocation_{fr}$). Wet (3154 mm yr^{-1} - 2050 mm yr^{-1}), semi-deciduous and deciduous (1740 mm yr^{-1} – 1310 mm yr^{-1}) lowland forests (left panels) are ordered from highest (left) to lowest (right) mean annual precipitation (mm yr^{-1}), which is shown on the upper x axis. The montane tropical forests (right panels) are ordered from lowest to highest elevations and grey shaded area indicates the cloud base at 1600 m asl (consistent with Malhi et al., 2017). Forest type designations of the plots followed Rifai et al. 2018. Note the different y-axis scales for lowland and montane forests. In some tropical forests, some aspects of fine root dynamics data were not recorded and the missing data is denoted with an asterisk (*). For the list of the plots and their characteristics, see Table 4.1.

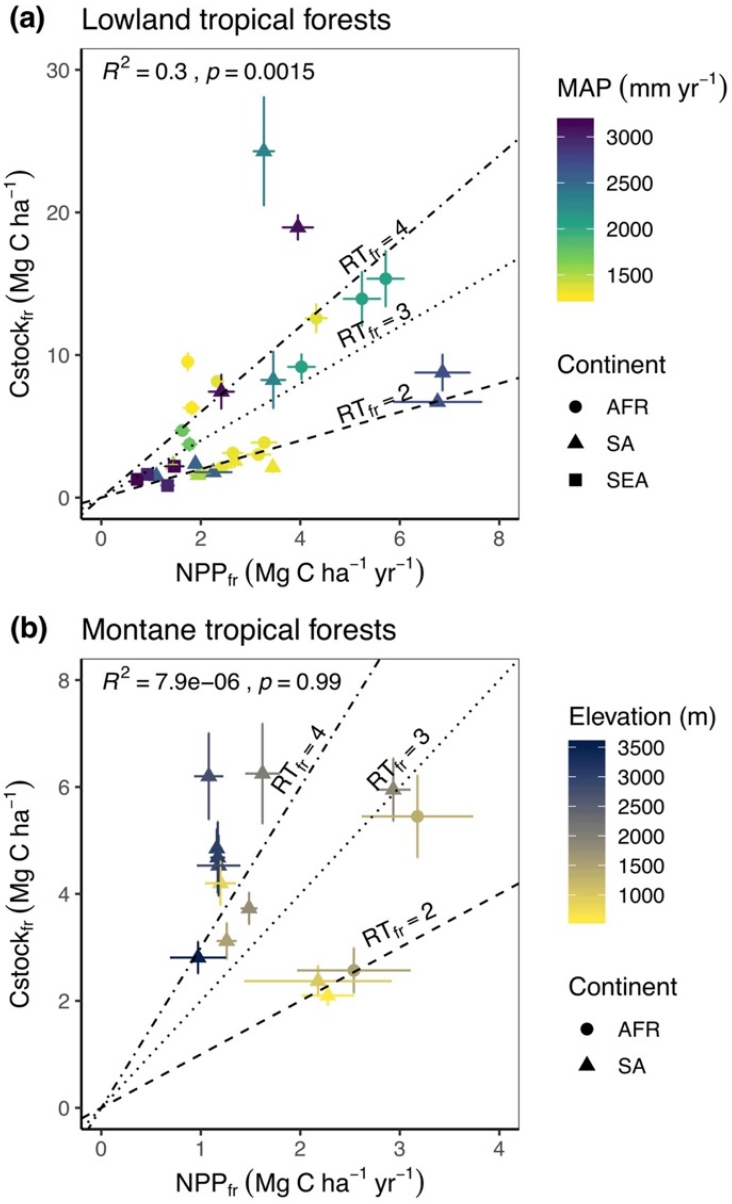


Figure 4.3. Relationships between fine root carbon stock ($Cstock_{fr}$) and productivity (NPP_{fr}) in (a) wet, semi-deciduous, and deciduous lowland tropical forests, coloured by mean annual precipitation (MAP) and, (b) montane tropical forests (MTF), coloured by elevation. The slope of dot dash (RT = 4), dotted (RT = 3), and dashed (RT = 2) lines through the origin indicate fine root residence times ($RT = Cstock_{fr}/NPP_{fr}$). The error bars show the standard error of the mean. Continent legend shows the African (AFR), South American (SA), and Southeast Asian (SEA) study sites.

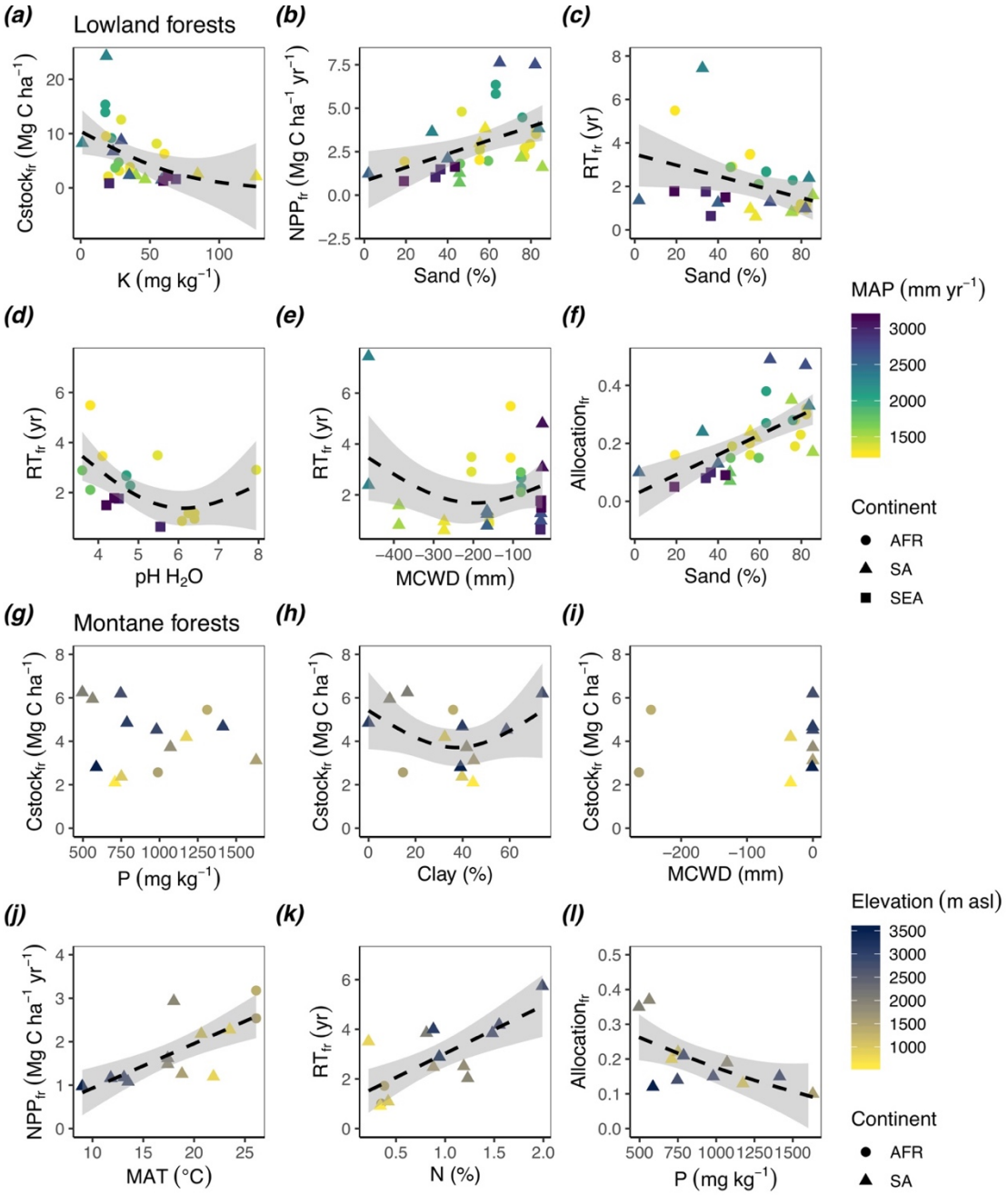


Figure 4.4. Generalised additive model (GAM) predictions of fine root biomass ($Cstock_{fr}$), productivity (NPP_{fr}), residence time (RT_{fr}), and allocation for lowland tropical forests (a, b, c, d, f) and for montane tropical forests (g, h, i, j, k, l) in relation to total soil potassium (K, mg kg^{-1}), soil phosphorus (P, mg kg^{-1}), soil nitrogen (N, %), mean annual temperature (MAT, ^{o}C), potential of hydrogen (pH H_2O), maximum cumulative water deficit (MCWD, mm yr^{-1}), soil clay content (%), and soil sand texture content (%). For model coefficients see Table 4.2. Dashed lines indicate the GAM model predictions and grey bands show the 95% confidence interval for the predictions. Soil data are integrated over 0-30 cm depth. Continent legend shows the African (AFR), South American (SA), and Southeast Asian (SEA) GEM study sites. Lowland sites (a, b, c, d, f) are coloured by mean annual precipitation (MAP) and montane sites (g, h, i, j, k, l) by elevation.

4.4 Discussion

4.4.1 Fine root dynamics variation across tropical rainforest

Fine root dynamics varied from wet to deciduous lowland forests, but in montane forests fine root C stock and residence time increased with increasing elevation and fine root productivity increased with decreasing elevation (Figure 4.3). Table 4.4 presents estimates of fine root C stock, productivity, residence time, and fractional allocation available in the current literature in tropical forests. We found clear trends across lowland tropical forests of highest fine root productivity, residence time, and carbon allocation in sites with high soil sand content (This study; Cavelier, 1992; Jiménez et al., 2009; Metcalfe et al., 2008; Noguchi et al., 2014; Pavlis & Jeník, 2000; Silver et al., 2000). However, the Bornean wet forests had the lowest NPP_{fr} averages for lowland plots, and these rates are similar to previous studies (Green et al., 2005; Kho et al., 2013; Kochsiek et al., 2013).

In montane tropical forests, the trends of fine root dynamics are more complex. Fine root C stock increased with increasing elevation in tropical montane regions of Costa Rica, Ecuador, Ethiopia, Indonesia, Peru, Malaysia, Rwanda, and Venezuela (This study; Assefa et al., 2017; Hertel et al., 2009; Ibrahima et al., 2010; Leuschner et al., 2007; Moser et al., 2010; Okada et al., 2017; Priess et al., 1999). We also found high root C stocks in the nutrient poor sites at the cloud base zone with low soil P. Root residence time increased with elevation, responding to the high soil organic matter and N content, while fine root productivity decreased with elevation.

Fine root residence time in both lowland and montane forests also depends on the proportion of the smaller-diameter, shorter-lived absorptive roots and the larger-diameter, longer-lived transport roots; their size difference is species-specific (Joslin et al., 2006; McCormack et al., 2015; Wang et al., 2019) and likely to vary among soil types (Cusack et al., 2020; Ibrahima et al., 2010; Telles et al., 2003). Therefore, the mean residence time in each

site is influenced by the species composition and the relative proportion and size distribution of the different root types, which we do not quantify in this study.

Soil texture played a key role in fractional allocation of total NPP to fine roots across lowland forests; allocation was higher in sandy soils than in clay, which may reflect the decrease in carbon allocation to stem and canopy productivity (Aragão et al., 2009; Kochsiek et al., 2013; Metcalfe et al., 2008). Allocation to fine roots also increased with decreasing soil P and N content (Pregitzer et al., 1995; Wright et al., 2011).

Malhi et al. (2011) estimated average tropical forest NPP allocation of 34% to canopy, 39% to woody tissue, and 27% to fine roots, with a considerable variation across sites and regions. In Southeast Asia, NPP allocation to fine roots ranged between 10% and 14% for old-growth lowland dipterocarp forests (Kho et al., 2013; Riutta et al., 2018), and between 6% and 30% in Kinabalu montane forests (Okada et al., 2017). This small fractional allocation to fine roots in South East Asia may be due to the ectomycorrhizal symbionts of the dipterocarp trees, which enhance nutrient uptake (Brearley. 2012; Robinson et al., 2020). In West African forests allocation to fine roots ranged between 22% and 33% (Moore et al., 2018; Morel et al., 2019), similar rates were reported for a previous Amazon basin study (Malhi et al., 2017). According to previous studies and this study, allocation to fine roots in lowland and montane forests across the tropics is driven by soil texture and nutrient content. Understanding belowground processes is particularly important for understanding the functioning of tropical forests on poor soils, where the fractional allocation of total NPP to fine roots is high.

Is allocation a better predictor of NPP_{fr} than absolute values of NPP_{fr}? The GEM approach of quantifying total NPP (instead of studying root productivity in isolation) provide a unique opportunity to quantify allocation of NPP between components. This allows us to distinguish if root productivity is low because of low overall NPP, or because a smaller proportion of the total NPP is allocated fine root production. In lowland forests, our results

indicate that allocation is more predictable than root productivity alone, and that the sand content is the strongest driver of NPP allocation to roots (Figure 4.4; Table 4.3). Sandy soils are more penetrable by fine roots but also have less water retention, and therefore the fractional allocation of total NPP to fine roots appears to be a clear priority at the expense of above-ground productivity. In montane forests, on the other hand, NPP_{fr} appears to be better predicted than $Allocation_{fr}$. This suggests that in montane forests fine root productivity rates are directly determined or limited by environmental conditions, and do not exhibit resource allocation trade-offs against above-ground components of NPP. This suggests that root productivity may be a particularly high priority in montane systems that is not subject to allocation trade-of.

Table 4.4. Fine root carbon stock ($Cstock_{fr}$), productivity (NPP_{fr}), residence time (RT_{fr}), and fractional allocation of total net primary productivity to fine roots ($Allocation_{fr}$) recorded by forest types of wet (WTF), semi-deciduous (SDTF), deciduous (DTF), and montane (MTF) tropical forests ecosystems.

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	$Cstock_{fr}$ (Mg C ha^{-1})	NPP_{fr} (Mg C ha^{-1} yr^{-1})	RT_{fr} (yr)	$Allocation_{fr}$ (%)	Reference
Colombia	Logged forest 18 years old, low terraces	WTF		20	5.19				Rev. in Jiménez et al. 2009
Colombia	Logged forest of 25 years old, low terraces	WTF		20	4.55				Rev. in Jiménez et al. 2009
Colombia	Logged forest of 37 years old, low terraces	WTF		20	6.83				Rev. in Jiménez et al. 2009
Colombia	Old forests in low terraces	WTF		20	12.40				Rev. in Jiménez et al. 2009
Colombia	Terra firme clay loam forest (Plinthosol)	WTF	105	20	2.46	2.45	1.01		Jiménez et al. 2009
Colombia	Terra firme clay loam forest (Plinthosol)	WTF	110	20	2.95	1.85	1.60		Jiménez et al. 2009
Colombia	Loamy sand forest	WTF	130	20	8.86	6.00	1.48		Jiménez et al. 2009
Colombia	Old growth forest	WTF	160	20	12.39				Pavlis J, Jeník J. 2000
Brazil	CAX-04	WTF	47	30	7.43	3.46	2.39	0.33	Present study
Brazil	CAX-06	WTF	47	30	21.86	3.27	7.44	0.24	Present study
Brazil	Lower slope in baixio	WTF	120	40	8.02				Noguchi et al. 2014
Brazil	Mid-slope	WTF	120	40	4.25				Noguchi et al. 2014
Brazil	Upper-slope	WTF	120	40	3.52				Noguchi et al. 2014
Brazil	Sand plot	WTF	50	30	5.67	1.80	3.15		Metcalfe et al. 2008
Brazil	Dry plot	WTF	50	30	4.05	1.35	3.00		Metcalfe et al. 2008
Brazil	Clay plot	WTF	50	30	6.08	1.80	3.38		Metcalfe et al. 2008
Brazil	Fertile plot	WTF	50	30	4.46	3.15	1.41		Metcalfe et al. 2008
Brazil	Sandy soil	WTF		10	1.82				Silver et al. 2000
Brazil	Clay soil	WTF		10	0.77				Silver et al. 2000
Ghana	ANK-01	WTF	114	30	13.81	5.72	2.68	0.38	Present study
Ghana	ANK-02	WTF	114	30	12.55	5.24	2.66	0.27	Present study
Ghana	ANK-03	WTF	78	30	8.25	4.02	2.28	0.28	Present study
Ivory Coast	Old growth forest (Banco P.)	WTF		30	5.10				Rev. in Cavalier et al. 1992
Ivory Coast	Old growth forest (Banco T.)	WTF		30	4.46				Rev. in Cavalier et al. 1992
Ivory Coast	Old growth forest (Yapo)	WTF		30	5.02				Rev. in Cavalier et al. 1992
Malaysia (Borneo)	Dipterocarp forest	WTF	200	15	0.69				Green et al. 2005
Malaysia (Borneo)	DAN-04	WTF		30	0.76	1.34	0.63	0.10	Present study
Malaysia (Borneo)	DAN-05	WTF		30	1.46	0.93	1.76	0.08	Present study
Malaysia (Borneo)	MLA-01	WTF		30	1.98	1.47	1.50	0.09	Present study
Malaysia (Borneo)	MLA-02	WTF		30	1.15	0.72	1.79	0.05	Present study
Peru	ALP-11	WTF	120	30	7.89	6.86	1.28	0.49	Present study
Peru	ALP-12	WTF	150	30	6.04	6.76	0.99	0.47	Present study
Peru	JEN-11	WTF	131	30	6.68	2.41	3.07		Present study
Peru	JEN-12	WTF	135	30	17.06	3.95	4.80		Present study
Peru	TAM-05	WTF	223	30	2.12	1.89	1.25	0.13	Present study
Peru	TAM-06	WTF	215	30	1.35	1.11	1.36	0.10	Present study
Peru	TAM-09	WTF	219	30	1.60	2.25	0.79		Present study
Republic of the Congo	Gallery forests	WTF	540	40	3.81				Suspense et al. 2015
Republic of the Congo	Hill-slope forest	WTF	540	40	1.74				Suspense et al. 2015

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	$Cstock_{fr}$ (Mg C ha^{-1})	NPP_{fr} (Mg C ha^{-1} yr^{-1})	RT_{fr} (yr)	$Allocation_{fr}$ (%)	Reference
Brazil	TAN-01	SDTF	385	30		1.14		0.10	Present study
Brazil	TAN-02	SDTF	385	30		0.64		0.07	Present study
Bolivia	KEN-01	SDTF	384	30	2.12	3.45	0.61	0.22	Present study
Bolivia	KEN-02	SDTF	384	30	2.57	2.68	0.96	0.24	Present study
Gabon	IVI-01	SDTF	578	30	3.74	1.77	2.11	0.15	Present study
Gabon	IVI-02	SDTF	458	30	4.71	1.63	2.90	0.15	Present study
Gabon	LPG-01	SDTF	406	30	9.53	1.74	5.47	0.16	Present study
Gabon	LPG-02	SDTF	302	30	6.29	1.82	3.46	0.20	Present study
Ghana	BOB-01	SDTF	235	30	8.15	2.33	3.50	0.16	Present study
Ghana	BOB-02	SDTF	235	30	12.58	4.32	2.91	0.19	Present study
Ghana	Old growth forest	SDTF	268	30	0.64				Addo-Danso et al. 2018
Ghana	Logged over forest	SDTF	276	30	1.37				Addo-Danso et al. 2018
Ghana	SDTF (Upper slope)	SDTF		30	1.71				Rev. in Cavalier et al. 1992
Ghana	SDTF (Middle slope)	SDTF		30	4.59				Rev. in Cavalier et al. 1992
Ghana	SDTF (Bottom slope)	SDTF		30	1.53				Rev. in Cavalier et al. 1992
Brazil	NXV-01	DTF	312	30	2.30	1.45	1.59	0.17	Present study
Brazil	NXV-02	DTF	324	30	1.59	1.94	0.82	0.35	Present study
Ghana	KOG-02	DTF	229	30	3.02	3.16	0.95	0.30	Present study
Ghana	KOG-03	DTF	229	30	3.86	3.28	1.18	0.32	Present study
Ghana	KOG-04	DTF	197	30	3.13	2.65	1.19	0.23	Present study
Ghana	KOG-05	DTF	221	30	2.12	2.42	0.87	0.28	Present study
Ghana	KOG-06	DTF	221	30	1.74	2.02	0.86	0.19	Present study
Ecuador	Lower montane forest	MTF	1050	25	1.22	1.63	0.75		Moser et al. 2010
Ecuador	Lower montane forest	MTF	1540	25	2.52	4.08	0.62		Moser et al. 2010
Ecuador	Lower montane forest	MTF	1890	25	2.79	3.16	0.88		Moser et al. 2010
Ecuador	Upper montane forest	MTF	2380	25	2.84	2.75	1.03		Moser et al. 2010
Ecuador	Upper montane forest	MTF	3060	25	4.86	1.67	2.92		Moser et al. 2010
Ecuador	Lower montane forest	MTF	1900	110	4.01				Soethe et al. 2007
Ecuador	Upper montane forest	MTF	2400	110	3.28				Soethe et al. 2007
Ecuador	Upper montane forest	MTF	3000	110	6.76				Soethe et al. 2007
Ecuador	Lower montane forest	MTF	1892	20		2.28			Röderstein et al. 2005
Ecuador	Upper montane forest	MTF	2380	20		5.52			Röderstein et al. 2005
Ecuador	Upper montane forest	MTF	3059	20		5.23			Röderstein et al. 2005
Ecuador	Lower montane forest	MTF	1050	30	1.21				Leuschener et al. 2007
Ecuador	Upper montane forest	MTF	3060	30	5.07				Leuschener et al. 2007
Ethiopia	Lower montane forest	MTF	1500	30	2.57	2.538	1.01		Present study
Ethiopia	Lower montane forest	MTF	1327	30	5.45	3.177	1.72		Present study
Indonesia	Pre-montane forest	MTF	1000	20	2.16				Hertel et al. 2009

Country	Description	Forest types	Elev (m)	Sampling depth (cm)	$Cstock_{fr}$ (Mg C ha^{-1})	NPP_{fr} (Mg C ha^{-1} yr^{-1})	RT_{fr} (yr)	$Allocation_{fr}$ (%)	Reference
Malaysia (Borneo)	Sedimentary montane forest	MTF	700	30	2.52				Kitayama & Aiba. 2002
Malaysia (Borneo)	Sedimentary montane forest	MTF	1700	30	4.28				Kitayama & Aiba. 2003
Malaysia (Borneo)	Sedimentary montane forest	MTF	2700	30	4.32				Kitayama & Aiba. 2004
Malaysia (Borneo)	Sedimentary montane forest	MTF	3100	30	4.59				Kitayama & Aiba. 2005
Malaysia (Borneo)	Ultrabasic montane forest	MTF	700	30	2.34				Kitayama & Aiba. 2006
Malaysia (Borneo)	Ultrabasic montane forest	MTF	1700	30	4.05				Kitayama & Aiba. 2007
Malaysia (Borneo)	Ultrabasic montane forest	MTF	2700	30	4.32				Kitayama & Aiba. 2008
Malaysia (Borneo)	Ultrabasic montane forest	MTF	3100	30	6.48				Kitayama & Aiba. 2009
Malaysia (Borneo)	Very short heath forest	MTF	1000	15	6.39				Miyamoto et al. 2016
Malaysia (Borneo)	Short heath forest	MTF	1000	15	5.63				Miyamoto et al. 2016
Malaysia (Borneo)	Mix dipterocarp transition forest	MTF	1000	15	4.01				Miyamoto et al. 2016
Malaysia (Borneo)	Small crow heath forest	MTF	500	15	2.79				Miyamoto et al. 2016
Malaysia (Borneo)	Large crown heath forest	MTF	500	15	2.57				Miyamoto et al. 2016
Malaysia (Borneo)	Mixed dipterocarp forest	MTF	500	15	1.71				Miyamoto et al. 2016
Malaysia (Borneo)	Sedimentary site	MTF	700	15	1.88	0.62	3.01	0.06	Okada et al. 2017
Malaysia (Borneo)	Sedimentary site	MTF	1700	15	2.50	0.72	3.45	0.12	Okada et al. 2017
Malaysia (Borneo)	Sedimentary site	MTF	2700	15	3.43	0.89	3.86	0.19	Okada et al. 2017
Malaysia (Borneo)	Sedimentary site	MTF	3100	15	3.69	0.32	11.44	0.08	Okada et al. 2017
Malaysia (Borneo)	Ultrabasic site	MTF	700	15	2.03	1.02	1.99	0.11	Okada et al. 2017
Malaysia (Borneo)	Ultrabasic site	MTF	1700	15	4.28	0.66	6.50	0.14	Okada et al. 2017
Malaysia (Borneo)	Ultrabasic site	MTF	2700	15	2.89	0.39	7.46	0.11	Okada et al. 2017
Malaysia (Borneo)	Ultrabasic site	MTF	3100	15	3.06	0.38	8.13	0.30	Okada et al. 2017
Malaysia (Borneo)	Quaternary site	MTF	1700	15	1.87	1.03	1.82	0.14	Okada et al. 2017
Peru	Pre-montane forest	MTF	595	30	2.10	2.28	0.92	0.2	Present study
Peru	Pre-montane forest	MTF	848	30	4.20	1.20	3.51	0.13	Present study
Peru	Pre-montane forest	MTF	1000	30	2.37	2.18	1.09	0.22	Present study
Peru	Lower montane forest	MTF	1527	30	3.12	1.26	2.48	0.1	Present study
Peru	Lower montane forest	MTF	1776	30	3.73	1.49	2.51	0.19	Present study
Peru	Lower montane forest	MTF	1885	30	5.95	2.93	2.03	0.37	Present study
Peru	Lower montane forest	MTF	2020	30	6.25	1.62	3.85	0.35	Present study
Peru	Upper montane forest	MTF	2758	30	6.20	1.08	5.74	0.14	Present study
Peru	Upper montane forest	MTF	3044	30	4.85	1.16	4.18	0.21	Present study
Peru	Upper montane forest	MTF	2863	30	4.53	1.18	3.84	0.15	Present study
Peru	Upper montane forest	MTF	3045	30	4.68	1.17	4.00	0.15	Present study
Peru	Upper montane forest	MTF	3537	30	2.81	0.97	2.89	0.12	Present study
Venezuela	High forest (Ferralsol)	MTF	1200	20	5.13	2.81	1.83		Priest et al. 1999
Venezuela	Medium forest (Ferralsol)	MTF	1201	20	5.49	2.75	1.99		Priest et al. 1999
Venezuela	Low forest (Ferralsol)	MTF	1202	20	4.33	3.78	1.15		Priest et al. 1999
Venezuela	Terra firme forest	MTF		30	6.21				Rev. in Jiménez et al. 2009
Venezuela	Bana	MTF		30	7.07				Rev. in Jiménez et al. 2009
Venezuela	Transitional forest Caatinga/Bana (Podzol)	MTF		30	7.07				Rev. in Jiménez et al. 2009
Venezuela	Caatinga	MTF		30	8.06				Rev. in Jiménez et al. 2009
Venezuela	Transitional forest TF/Catinga (Podzol)	MTF		30	17.78				Rev. in Jiménez et al. 2009

4.4.2 The effect of soil chemical properties on fine root dynamics

One remarkable result of our study is that climate variables hardly feature as explanatory variables for fine root dynamics. Instead, soil texture and chemistry dominate as explanatory factors. Soil nutrient content and texture are key drivers of fine root dynamics across the tropical forests monitored by the GEM network. In particular, we identified soil sand content and N, P, and K concentration as the main soil properties that drive fine root dynamics across the tropics.

Decreasing total soil K was correlated with increased fine root C stock across the lowland forest types. This was related to K limitation in our study sites, whereby ecosystems with high soil sand content are more K limited and, therefore, have higher root C stock. Such ecosystems need to store more K in their root systems, and forage deeper to access K stores in the soil (Sardans & Peñuelas, 2015; Soethe et al., 2007). This is confirmed by long-term soil fertilization experiments in lowland wet tropical forests in Panama that showed a decline in root C stock in response to elevated K (Cusack et al., 2018; Yavitt et al., 2011). Also, the addition of K reduced fine root C stock at the community level, reduced allocation to roots, and increased tree height growth rates (Wright et al., 2011). Hence, we conclude that soil sand content and K are negatively correlated across the lowland forests, and lowland tropical tree species have to invest more energy to increase the fractional allocation to roots in sandy soil forests.

Soil N content was positively correlated with fine root residence time in montane forests. Our calculated variation in root residence time in the montane forests is more strongly driven by the variation in root C stock than by the variation in root productivity (Figure 4.2b). Some studies reported that soil N deficiency is expected to increase fine root C stock and longevity, and soil N availability decreased from 1050 to 3060 m asl due to decreasing N mineralization and concentration of inorganic sources (Graefe et al., 2010; Moser et al., 2011).

Nitrogen inputs to the soil depends on the symbiotic N fixation rates of N fixing tree species, and high N use efficiency is associated with tropical white-sand and montane forests with low rates of N circulation (Hedin et al., 2009; Menge et al., 2019; Pajares & Bohannan, 2016). Overall, our montane forest results support the constant allocation hypothesis of Hendricks et al. (1993) that root residence time increases with increasing N soil availability.

We identified P as a key determinant of the fractional allocation of total NPP to fine roots in montane forests. Phosphorus is the most limiting soil nutrient component in tropical forests after N and K (Laliberté et al., 2015; Lugli et al., 2019; Quesada et al., 2009). Fine root C stock, longevity, and total length increased in response to P deficiency in montane forests in Malaysian Borneo (Kitayama, 2013; Okada et al., 2017; Ushio et al., 2015). The limiting P supply means that at the plot level, morphological traits that facilitate P uptake are favoured on soils of low P (Addo-Danso et al., 2020), which could be due to the plasticity of the species traits or due to the community shift. Plants also develop rhizosphere and mycorrhizal fungi symbioses in response to persistent P deficiency (Raghothama & Karthikeyan, 2005). Between 1885 and 2020 m asl (cloud base range), we recorded the highest fractional allocation to fine roots that ranged between 39% and 41%, rates comparable to those found in lower montane forest with low P availability in the South American Andes (Moser et al., 2011). Ushio et al. (2015) suggested that high allocation to fine roots in mid-elevation montane forests is an adaptation to soils with low P availability by increasing specific root surface and longevity. Diffusion of P in nutrient poor tropical soils is particularly slow because high concentration of Al, iron oxides, and hydroxide drive the fast absorption of P (Laliberté et al., 2015; Ushio et al., 2015). Also, fertilization experiment revealed that litterfall content of P and N is lower on wet tropical forest above 1500 m asl (Tanner, Vitousek, & Cuevas, 1998).

Sand content of the soil was the main determinant of fine root productivity, residence time, and fractional allocation of total NPP to fine roots across lowland rainforest ecosystems.

Sandy soil forests assign more biomass, length, and surface area to fine roots through faster growth and greater investment in root dynamics. This is probably due to the lower nutrient and water holding capacity of the sandy soils, compared with clay soils (Kochsiek et al., 2013; Nepstad et al., 1994). Soil respiration in sandy soils is higher than in clay soils, which may be an indicator of high fine root productivity and allocation across tropical lowland forests (Silver et al., 2005; Sotta et al., 2006). Root decay rates are also lower in sandy soils than in clay soils due to water and nutrient limitation and lower decomposer diversity (Silver et al., 2005). According to our results and previous studies, forests with high soil sand content have high fractional allocation of total NPP to fine roots, as a response to low nutrient availability in lowland forest soils (Aragão et al., 2009; Jiménez et al., 2009; Kochsiek et al., 2013; Quesada et al., 2012; Silver et al., 2000; Yavitt et al., 2011). On sandy soils, most lowland tropical wet forests produce litter low in N and on clay soil, low in P (Cavelier, 1992; Tanner et al., 1998).

Soil clay content was another significant predictor of fine root C stock in montane forests in our study. In previous studies, soil clay content and root biomass were significant predictors of soil carbon stock in humid tropical forests in Panama (Cusack et al., 2018), and clay content had a positive correlation with soil organic carbon concentration (Quesada et al., 2020) and with old soil carbon stock (Telles et al., 2003) in lowland forests in the Amazon. Root mortality and root exudates constitute the majority of the organic carbon inputs into the soil (Girardin et al., 2013; Graefe et al., 2008a, 2008b; Zimmermann et al., 2009), with recent inputs detected even in the subsoil (>30 cm depth) (Balesdent et al., 2018). Approximately 50% of soil carbon exceeds the age of 100 years in the top 30 cm layer in the tropics (Balesdent et al., 2018). The persistence of these organic carbon inputs in the soil over time is strongly linked to adsorption and soil texture (Lehmann and Kleber et al., 2015), with clay minerals being important in the retention and stabilisation of soil organic carbon (Singh et al., 2018).

Soil pH emerged as the second soil property after soil sand texture that drives root residence time in lowland forests, residence time increasing with increasing soil acidity (Figure 4.4d). Two previous studies in tropical forests reported that soil acidity was negatively correlated with fine root biomass, and high fine root productivity originated from the necessity of plants to uptake nutrients in strongly acidic soils (Hertel et al., 2009; Priess et al., 1999). High soil acidity across lowland old-growth forests may also increase the soil Aluminium content (see the soil PCA analysis in Figure S4.1 and Table S4.1), therefore, the lower fine root biomass and longer residence time in low pH soils may also be due to the increased Al toxicity. Al is known for its negative effect on root-tips and root elongation in mineral soil, which reduces roots growth (Delhaize et al., 2012; Gupta et al., 2013; Rout et al., 2001). The negative effect of the Al stress on root morphology has been demonstrated on tree seedlings in tropical montane forests and (Rehmus et al., 2014) and should be explored on fine root trait studies across a wider range of tropical forests.

4.4.3 The effect of climatic variables on fine root dynamics

Our analyses revealed that MAT and MCWD are related to fine root dynamics across the tropical forests, although these drivers were not as strong as soil texture and chemistry. MAT had a positive effect on fine root productivity in montane forests. A similar effect was reported on root net primary productivity in Ecuadorian and Bornean montane forests (Moser et al., 2010; Okada et al., 2017). In previous studies, decreasing temperature increased root residence time, resulting in a decrease in fine root decomposition, mineralization, and nitrification with increasing elevation in poorly developed and high acidity montane forests (Graefe et al., 2008b; Reich et al., 2014; Sierra Cornejo et al., 2020). The tropical montane trees respond by producing more fine roots to uptake nutrients in low nutrient soils and MAT drives the fine root productivity in montane forests.

Whereas most of fine root dynamics studies across lowland forests recorded a positive relationship between precipitation and fine root biomass and productivity at a regional scale (Cusack et al., 2018; Green et al., 2005; Kho et al., 2013; Violita et al., 2016). In western Ghana, root biomass study along a precipitation gradient from dry to wet lowland forests revealed that $Cstock_{fr}$ increased with increasing MAP (Ibrahim et al., 2020). We did not find any significant pantropical relationships for precipitation and fine root dynamics. Yet, the annual maximum cumulative water deficit slightly increased fine root residence time across lowland forests.

4.4.4 Methodological considerations

Soil cores and ingrowth cores are a widely applied methods that provide direct estimates of root bomass and productivity, we acknowledge the uncertainties and limitations associated with these methods. Firstly, the sampling depth is limited, in our case 30 cm, which leads to an underestimate of fine root biomass and productivity. The reported proportions of the fine root biomass in the top 30 cm soil layer out of total biomass range between 42% and 57% in tropical forests (Jackson et al., 1997), some new studies reported 46% in Amazon forests (Cordeiro et al., 2020) and ~44% in Africa (Ibrahima et al., 2010). The data on the depth profile of fine root productivity is more limited, with 60% within the top 30 cm reported for Central Amazon (Cordeiro et al., 2020). Residence time within the top 30 cm compared with the whole soil profile is also likely to be an underestimate, as the life span of the deeper fine roots exceeds that of shallower roots (Cordeiro et al., 2020). Secondly, the ingrowth core method may underestimate productivity, particularly in systems where root turnover is high (Hendricks et al., 2006; Katayama et al., 2019). We collect both living and dead roots from the ingrowth cores (the dead roots would have been alive within the three-month interval, as we start with root free soil), and our collection interval, three months, is relatively short, which decreases this bias. Katayama et al. (2019) estimated that approximately 7% of the fine roots decomposed

fully within a three-month period in a Bornean forest. Thirdly, the installation of the core causes disturbance, which causes additional noise in the data, and possibly an over-estimate in the short-term root production due to reduced competition in the initially root-free soil and the proliferation of adventitious roots due to the root severing at the installation (e.g. Vogt et al., 1998; Hendricks et al. 2006). Despite the short-comings of the method, however, we have found we have found good agreement between the ingrowth core and screen rhizotron techniques, collected in a subset of these sites (Huaraca Huasco et al. in prep).

4.4.5 Conclusions

We quantified fine root dynamics and investigating the relationships between fine root dynamics, soil nutrient content, and climatic variables in montane and lowland tropical rainforest ecosystems in three continents. One remarkable feature of our results is that soil physics and chemistry are the strongest drivers of root dynamics, whereas climate variables hardly feature as explanatory variables.

We found a strong positive linear relationship between fine root productivity and soil sand content. This positive relationship was even stronger when we considered fine root allocation as a fraction of total NPP, demonstrating that understanding of total NPP adds explanatory power to understanding fine root productivity. Fine root residence time was a function of multiple factors: soil sand content, soil pH, and maximum water deficit, with longest residence times in acidic, sandy and water-stressed soils in lowland forests. In montane forests, fine root productivity was a strong positive linear function of mean annual temperature, fine root residence time was a strong positive function of soil nitrogen content, and fractional allocation of total NPP to fine roots increased with decreasing soil P availability. In contrast to the lowlands, environmental conditions were a better predictor of fine root productivity than of fractional allocation to fine roots root, suggesting that fine root productivity may be a dominant driver of NPP allocation in tropical mountain regions.

Our understanding of global fine root dynamics needs refining. A logical next step to understand the effect of drought events across the tropics would be to expand this analysis to seasonal variation of root dynamics. There are important gaps in our understanding of the belowground ecosystem functioning of tropical forests, and how they will respond to rapidly changing climate.

4.5 Acknowledgements

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4.6 References

Addo-Danso, S. D., Defrenne, C. E., McCormack, M. L., Ostonen, I., Addo-Danso, A., Foli, E. G., Borden, K. A., Isaac, M. E., & Prescott, C. E. (2020). Fine-root morphological trait variation in tropical forest ecosystems: an evidence synthesis. *Plant Ecology*, 221: 1-13. https://doi.org/10.1007/s11258-019-00986-1

Addo-Danso, S. D., Prescott, C. E., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Guy, R. D., ... & Malhi, Y. (2018). Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. *Biotropica*, *50*(4), 606-615. http://doi.wiley.com/10.1111/btp.12556

Addo-Danso, S. D., Prescott, C. E., Smith, A. (2016). Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A Review. *Forest Ecology & Management*, 359: 332-351. http://dx.doi.org/10.1016/j.foreco.2015.08.015

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Aragão, Luiz Eduardo O.C., Malhi, Y., Roman-Cuesta, R. M., Saatchi, S., Anderson, L. O., & Shimabukuro, Y. E. (2007). Spatial patterns and fire response of recent Amazonian droughts. *Geophysical Research Letters*, *34*(7), 1–5. https://doi.org/10.1029/2006GL028946

Araujo-Murakami, A., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., … Malhi, Y. (2014). The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecology & Diversity*, *7*(1–2), 55–69. https://doi.org/10.1080/17550874.2013.798364

Assefa, D., Rewald, B., Sandén, H., & Godbold, D. L. (2017). Fine Root Dynamics in Afromontane Forest and Adjacent Land Uses in the Northwest Ethiopian Highlands. *Forests*, *8*(7), 249. https://doi.org/10.3390/f8070249

Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., & Hatté, C. (2018). Atmosphere–soil carbon transfer as a function of soil depth. *Nature*, *559*(7715), 599–602. https://doi.org/10.1038/s41586-018-0328-3

Barbosa, R. I., Santos, J. R. S. dos, Cunha, M. S. da, Pimentel, T. P., & Fearnside, P. M. (2012). Root biomass, root: shoot ratio and belowground carbon stocks in the open savannahs of Roraima, Brazilian Amazonia. *Australian Journal of Botany*, *60*, 405–416. https://doi.org/10.1071/BT11312

Barton, K., & Barton, M. K. (2015). Package 'mumin'. *Version*, *1*, 18. ftp://xyz.csail.mit.edu/pub/CRAN/web/packages/MuMIn/MuMIn.pdf

Brearley, F. Q. (2012). Ectomycorrhizal Associations of the Dipterocarpaceae. *Biotropica*, *44*(5), 637–648. https://doi.org/10.1111/j.1744-7429.2012.00862.x

Castanho, A. D. A., Coe, M. T., Costa, M. H., Malhi, Y., Galbraith, D., & Quesada, C. A. (2013). Improving simulated Amazon forest biomass and productivity by including spatial variation in biophysical parameters. *Biogeosciences*, *10*(4), 2255–2272. https://doi.org/10.5194/bg-10-2255-2013

Cavelier, J. (1992). Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama. *Plant and Soil*, *142*(2), 187–201. https://doi.org/10.1007/BF00010965

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde- Barrantes, O., Fuchslueger, L., Oblitas Mendoza, E., Hartley, I., Iversen, C. M., Goncalves, N., Takeshi, B., Lapola, D. M., & Quesada, C. A. (2020). Fine- root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. Plant- Environment Interactions,

1(1), 3–16. https://doi.org/10.1002/pei3.10010
Cusack, D. F., Markesteijn, L., Condit, R., Lewis, O. T., & Turner, B. L. (2018). Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots. *Biogeochemistry*, *137*(1–2), 253–266. https://doi.org/10.1007/s10533-017-0416-8
Cusack, D. F., & Turner, B. L. (2020). Fine Root and Soil Organic Carbon Depth Distributions are Inversely Related Across Fertility and Rainfall Gradients in Lowland Tropical Forests. *Ecosystems*, 1–18. https://doi.org/10.1007/s10021-020-00569-6
da Costa, A. C. L., Metcalfe, D. B., Doughty, C. E., de Oliveira, A. A. R., Neto, G. F. C., da Costa, M. C., … Malhi, Y. (2014). Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest. *Plant Ecology & Diversity*, *7*(1–2), 7–24. https://doi.org/10.1080/17550874.2013.798366
del Aguila-Pasquel, J., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Girardin, C. A. J., Chung Gutierrez, J. A., … Malhi, Y. (2014). The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology & Diversity*, *7*(1–2), 71–83. https://doi.org/10.1080/17550874.2013.798365
Delhaize, E., Ma, J. F., & Ryan, P. R. (2012). Transcriptional regulation of aluminium tolerance genes. *Trends in Plant Science*, *17*(6), 341–348. https://doi.org/10.1016/j.tplants.2012.02.008
Doughty, C. E., Goldsmith, G. R., Raab, N., Girardin, C. A. J., Farfan-Amezquita, F., Huaraca-Huasco, W., … Malhi, Y. (2018). What controls variation in carbon use efficiency among Amazonian tropical forests? *Biotropica*, *50*(1), 16–25. https://doi.org/10.1111/btp.12504
Ewers, R. M., Didham, R. K., Fahrig, L., Ferraz, G., Hector, A., Holt, R. D., … Turner, E. C. (2011). A large-scale forest fragmentation experiment: The Stability of Altered Forest Ecosystems Project. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1582), 3292–3302. https://doi.org/10.1098/rstb.2011.0049
Feng, X., Porporato, A., & Rodriguez-Iturbe, I. (2013). Changes in rainfall seasonality in the tropics. *Nature Climate Change*, *3*(9), 811–815. https://doi.org/10.1038/nclimate1907
Finér, L., Ohashi, M., Noguchi, K., & Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management*, *262*(11), 2008–2023. https://doi.org/10.1016/j.foreco.2011.08.042
Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, *147*(1), 13–31. https://doi.org/10.1046/j.1469-8137.2000.00681.x
Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082
Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., … Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*(12), 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x
Girardin, C. A. J., Silva Espejo, J. E., Doughty, C. E., Huaraca Huasco, W., Metcalfe, D. B., Durand-Baca, L., … Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222
Gupta, N., Gaurav, S. S., & Kumar, A. (2013). Molecular Basis of Aluminium Toxicity in Plants: A Review. *American Journal of Plant Sciences*, *04*(12), 21–37. https://doi.org/10.4236/ajps.2013.412A3004
Graefe, S., Hertel, D., & Leuschner, C. (2008a). Estimating Fine Root Turnover in Tropical Forests along an Elevational Transect using Minirhizotrons. *Biotropica*, *40*(5), 536–542.

https://doi.org/10.1111/j.1744-7429.2008.00419.x
Graefe, S., Hertel, D., & Leuschner, C. (2008b). Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil*, *313*(1–2), 155–166. https://doi.org/10.1007/s11104-008-9688-z
Graefe, S., Hertel, D., & Leuschner, C. (2010). N, P and K limitation of fine root growth along an elevation transect in tropical mountain forests. *Acta Oecologica*, *36*(6), 537–542. https://doi.org/10.1016/j.actao.2010.07.007
Green, J. J., Dawson, L. A., Proctor, J., Duff, E. I., & Elston, D. A. (2005). Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. *Plant and Soil*, *276*(1–2), 23–32. https://doi.org/10.1007/s11104-004-0331-3
Gvozdevaite, A., Oliveras, I., Domingues, T. F., Peprah, T., Boakye, M., Afriyie, L., … Malhi, Y. (2018). Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–savanna boundaries in Ghana and Brazil. *Tree Physiology*, *38*(12), 1912–1925. https://doi.org/10.1093/treephys/tpy117
Hedin, L. O., Brookshire, E. N. J., Menge, D. N. L., & Barron, A. R. (2009). The Nitrogen Paradox in Tropical Forest Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 613–635. https://doi.org/10.1146/annurev.ecolsys.37.091305.110246
Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., & Guo, D. (2006). Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology*, *94*(1), 40–57. https://doi.org/10.1111/j.1365-2745.2005.01067.x
Hendricks, J. J., Nadelhoffer, K. J., & Aber, J. D. (1993). Assessing the role of fine roots in carbon and nutrient cycling. *Trends in Ecology and Evolution*, *8*(5), 174–178. https://doi.org/10.1016/0169-5347(93)90143-D
Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., & Leuschner, C. (2009). Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. *Forest Ecology and Management*, *258*(9), 1904–1912. https://doi.org/10.1016/j.foreco.2009.07.019
Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, 7(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042
Ibrahim, F., Adu-Bredu, S., Addo-Danso, S. D., Duah-Gyamfi, A., Manu, E. A., & Malhi, Y. (2020). Patterns and controls on fine-root dynamics along a rainfall gradient in Ghana. *Trees*, 1–13. https://doi.org/10.1007/s00468-020-01970-3
Ibrahima, A., Mvondo ZE, A., & Ntonga, J. (2010). Fine root production and distribution in the tropical rainforests of south-western Cameroon: effects of soil type and selective logging. *iForest - Biogeosciences and Forestry*, *3*(5), 130–136. https://doi.org/10.3832/ifor0549-003
Ifo, S. A., Koubouana, F., Nganga, D., Bocko, Y., & Mantota, A. (2015). Fine roots dynamics in a tropical moist forest: Case of two forest groves in the Congo Basin. Baltic Forestry, 21(2), 204– 211.
Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., … Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26. https://doi.org/10.1111/nph.14486
Jackson, R. B., Mooney, H. A., & Schulze, E. D. (1997). A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(14), 7362–7366. https://doi.org/10.1073/pnas.94.14.7362

Jiménez, E. M., Moreno, F. H., Lloyd, J., Peñuela, M. C., & Patiño, S. (2009). Fine root dynamics for forests on contrasting soils in the colombian Amazon. *Biogeosciences Discussions*, *6*(2), 3415–3453. https://doi.org/10.5194/bgd-6-3415-2009

Joslin, J. D., Gaudinski, J. B., Torn, M. S., Riley, W. J., & Hanson, P. J. (2006). Fine-root turnover patterns and their relationship to root diameter and soil depth in a ^{14}C-labeled hardwood forest. *New Phytologist*, *172*(3), 523–535. https://doi.org/10.1111/j.1469-8137.2006.01847.x

Kassambara, A., & Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. Package Version 1.0.7. *R Package Version*. Retrieved from https://cran.r-project.org/web/packages/factoextra/factoextra.pdf

Katayama, A., Kho, L. K., Makita, N., Kume, T., Matsumoto, K., & Ohashi, M. (2019). Estimating Fine Root Production from Ingrowth Cores and Decomposed Roots in a Bornean Tropical Rainforest. *Forests*, *10*(1), 36. https://doi.org/10.3390/f10010036

Kho, L. K., Malhi, Y., & Tan, S. K. S. (2013). Annual budget and seasonal variation of aboveground and belowground net primary productivity in a lowland dipterocarp forest in Borneo. *Journal of Geophysical Research: Biogeosciences*, *118*(3), 1282–1296. https://doi.org/10.1002/jgrg.20109

Kitayama, K. (2013). The activities of soil and root acid phosphatase in the nine tropical rain forests that differ in phosphorus availability on Mount Kinabalu, Borneo. *Plant and Soil*, *367*(1–2), 215–224. https://doi.org/10.1007/s11104-013-1624-1

Kitayama, K., & Aiba, S. (2002). Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus on Mount Kinabalu, Borneo. *Journal of Ecology*, *90*, 37–51. https://www.jstor.org/stable/3072317

Kochsiek, A., Tan, S., & Russo, S. E. (2013). Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology*, *214*(6), 869–882. https://doi.org/10.1007/s11258-013-0215-9

Laliberté, E., Lambers, H., Burgess, T. I., & Wright, S. J. (2015). Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist*, *206*(2), 507–521. https://doi.org/10.1111/nph.13203

Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, *528*(7580), 60–68. https://doi.org/10.1038/nature16069

Leuschner, C., Moser, G., Bertsch, C., Röderstein, M., & Hertel, D. (2007). Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology*, *8*(3), 219–230. https://doi.org/10.1016/j.baae.2006.02.004

Lugli, L. F., Andersen, K. M., Aragão, L. E. O. C., Cordeiro, A. L., Cunha, H. F. V., Fuchslueger, L., … Hartley, I. P. (2019). Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil*, *450*(1–2), 49–63. https://doi.org/10.1007/s11104-019-03963-9

Majdi, H., Pregitzer, K., Morén, A.-S., Nylund, J.-E., & I. Ågren, G. (2005). Measuring Fine Root Turnover in Forest Ecosystems. *Plant and Soil*, *276*(1–2), 1–8. https://doi.org/10.1007/s11104-005-3104-8

Malhi, Y., Aragão, L. E. O. C., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., … Teixeira, L. M. (2009). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, *15*(5), 1255–1274. https://doi.org/10.1111/j.1365-2486.2008.01780.x

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1582), 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B.,

… Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E. O. C., Rifai, S. W., … Phillips, O. L. (2021). The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. *Biological Conservation*, *253*, 108889. https://doi.org/10.1016/j.biocon.2020.108889

Marthews, T. R., Riutta, T., Menor, I. O., Urrutia, R., Moore, S., Metcalfe, D., … Networks, C. R. and colleagues from the R. and G. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0, 121. http://gem.tropicalforests.ox.ac.uk

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., … Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *The New Phytologist*, *207*(3), 505–518. https://doi.org/10.1111/nph.13363

McCormack, M. L., Lavely, E., & Ma, Z. (2014). Fine-root and mycorrhizal traits help explain ecosystem processes and responses to global change. *New Phytologist*, *204*(3), 455–458. https://doi.org/10.1111/nph.13023

Menge, D. N. L., Chisholm, R. A., Davies, S. J., Abu Salim, K., Allen, D., Alvarez, M., … Fung, T. (2019). Patterns of nitrogen-fixing tree abundance in forests across Asia and America. *Journal of Ecology*, *107*(6), 2598–2610. https://doi.org/10.1111/1365-2745.13199

Metcalfe, D. B., Williams, M., Aragão, L. E. O. C., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., … Meir, P. (2007). A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. *New Phytologist*, *174*(3), 697–703. https://doi.org/10.1111/j.1469-8137.2007.02032.x

Metcalfe, D. B., Meir, P., Aragão, L. E. O. C., da Costa, A. C. L., Braga, A. P., Gonçalves, P. H. L., … Williams, M. (2008). The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, *311*(1–2), 189–199. https://doi.org/10.1007/s11104-008-9670-9

Moore, S., Adu-Bredu, S., Duah-Gyamfi, A., Addo-Danso, S. D., Ibrahim, F., Mbou, A. T., … Malhi, Y. (2018). Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. *Global Change Biology*, *24*(2), e496–e510. https://doi.org/10.1111/gcb.13907

Morel, A. C., Adu Sasu, M., Adu-Bredu, S., Quaye, M., Moore, C., Ashley Asare, R., … Malhi, Y. (2019). Carbon dynamics, net primary productivity and human-appropriated net primary productivity across a forest–cocoa farm landscape in West Africa. *Global Change Biology*, *25*(8), 2661–2677. https://doi.org/10.1111/gcb.14661

Morel, A. C., Hirons, M., Demissie, S., Gonfa, T., Mehrabi, Z., Long, P. R., … Norris, K. (2019). The structures underpinning vulnerability: Examining landscape-society interactions in a smallholder coffee agroforestry system. *Environmental Research Letters*, *14*(7). https://doi.org/10.1088/1748-9326/ab2280

Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N., & Iost, S. (2011). Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment. *Global Change Biology*, *17*(6), 2211–2226. https://doi.org/10.1111/j.1365-2486.2010.02367.x

Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., & Hertel, D. (2010). Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity*, *3*(2), 151–164. https://doi.org/10.1080/17550874.2010.517788

Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros,

G. H., ... & Vieira, S. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, *372*(6507), 666-669. https://doi.org/10.1038/372666a0

Noguchi, H., Suwa, R., Souza, C. A. S. de, Silva, R. P. da, Santos, J. dos, Niro, H., … Ishizuka, M. (2014). Examination of Vertical Distribution of Fine Root Biomass in a Tropical Moist Forest of the Central Amazon, Brazil. *Japan Agricultural Research Quarterly: JARQ*, *48*(2), 231–235. https://doi.org/10.6090/jarq.48.231

Okada, K., Aiba, S., & Kitayama, K. (2017). Influence of temperature and soil nitrogen and phosphorus availabilities on fine-root productivity in tropical rainforests on Mount Kinabalu, Borneo. *Ecological Research*, *32*(2), 145–156. https://doi.org/10.1007/s11284-016-1425-0

Pajares, S., & Bohannan, B. J. M. (2016). Ecology of Nitrogen Fixing, Nitrifying, and Denitrifying Microorganisms in Tropical Forest Soils. *Frontiers in Microbiology*, *7*, 1045. https://doi.org/10.3389/fmicb.2016.01045

Pavlis, J., & Jeník, J. (2000). Roots of pioneer trees in the Amazonian rain forest. *Trees*, *14*(8), 442–455. https://doi.org/10.1007/s004680000049

Peng, Y., Guo, D., & Yang, Y. (2017). Global patterns of root dynamics under nitrogen enrichment. *Global Ecology and Biogeography*, *26*(1), 102–114. https://doi.org/10.1111/geb.12508

Pregitzer, K. S., Zak, D. R., Curtis, P. S., Kubiske, M. E., Teeri, J. A., & Vogel, C. S. (1995). Atmospheric CO2, soil nitrogen and turnover of fine roots. *New Phytologist*, *129*(4), 579–585. https://doi.org/10.1111/j.1469-8137.1995.tb03025.x

Priess, J., Then, C., & Fölster, H. (1999). Litter and fine-root production in three types of tropical premontane rain forest in SE Venezuela. *Plant Ecology*, *143*(2), 171–187. https://doi.org/10.1023/A:1009844226078

Quesada, C. A., Paz, C., Oblitas Mendoza, E., Phillips, O., Saiz, G., & Lloyd, J. (2020). Variations in soil chemical and physical properties explain basin-wide variations in Amazon forest soil carbon densities. *Soil*, 1–62. https://doi.org/10.5194/soil-6-53-2020

Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., … Paiva, R. (2009). Chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences Discussions*, *6*(2), 3923–3992. https://doi.org/10.5194/bgd-6-3923-2009

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., … Lloyd, J. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, *9*(6), 2203–2246. https://doi.org/10.5194/bg-9-2203-2012

Raghothama, K. G., & Karthikeyan, A. S. (2005). Phosphate Acquisition. *Plant and Soil*, *274*(1–2), 37–49. https://doi.org/10.1007/s11104-004-2005-6

Rehmus, A., Bigalke, M., Valarezo, C., Castillo, J. M., & Wilcke, W. (2014). Aluminum toxicity to tropical montane forest tree seedlings in southern Ecuador: Response of biomass and plant morphology to elevated Al concentrations. *Plant and Soil*, *382*(1–2), 301–315. https://doi.org/10.1007/s11104-014-2110-0

Reich, P. B., Luo, Y., Bradford, J. B., Poorter, H., Perry, C. H., & Oleksyn, J. (2014). Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots. *Proceedings of the National Academy of Sciences*, *111*(38), 13721–13726. https://doi.org/10.1073/pnas.1216053111

Rifai, S. W., Girardin, C. A. J., Berenguer, E., del Aguila-Pasquel, J., Dahlsjö, C. A. L., Doughty, C. E., … Malhi, Y. (2018). ENSO Drives interannual variation of forest woody growth across the tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1760), 20170410. https://doi.org/10.1098/rstb.2017.0410

Riutta, T., Malhi, Y., Kho, L. K., Marthews, T. R., Huaraca Huasco, W., Khoo, M. S., … Ewers, R. M. (2018). Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. *Global Change Biology*, *24*(7), 2913–2928. https://doi.org/10.1111/gcb.14068

Robinson, S. J. B., Elias, D., Johnson, D., Both, S., Riutta, T., Goodall, T., … Ostle, N. (2020). Soil Fungal Community Characteristics and Mycelial Production Across a Disturbance Gradient in Lowland Dipterocarp Rainforest in Borneo. *Frontiers in Forests and Global Change*, *3*. https://doi.org/10.3389/ffgc.2020.00064

Rocha, W., Metcalfe, D. B., Doughty, C. E., Brando, P., Silvério, D., Halladay, K., … Malhi, Y. (2014). Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). *Plant Ecology & Diversity*, *7*(1–2), 25–40. https://doi.org/10.1080/17550874.2013.798368

Röderstein, M., Hertel, D., & Leuschner, C. (2005). Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, *21*(05), 483–492. https://doi.org/10.1017/S026646740500249X

Rout, G. R., Samantaray, S., & Das, P. (2001). Aluminium toxicity in plants: a review. *Agronomie*, *21*(1), 3–21. https://doi.org/10.1051/agro:2001105

Sardans, J., & Peñuelas, J. (2015). Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography*, *24*(3), 261–275. https://doi.org/10.1111/geb.12259

Sierra Cornejo, N., Hertel, D., Becker, J. N., Hemp, A., & Leuschner, C. (2020). Biomass, Morphology, and Dynamics of the Fine Root System Across a 3,000-M Elevation Gradient on Mt. Kilimanjaro. *Frontiers in Plant Science*, *11*, 13. https://doi.org/10.3389/fpls.2020.00013

Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., & Cosme, R. (2000). Effects of Soil Texture on Belowground Carbon and Nutrient Storage in a Lowland Amazonian Forest Ecosystem. *Ecosystems*, *3*(2), 193–209. https://doi.org/10.1007/s100210000019

Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., … Keller, M. (2005). Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology*, *11*(2), 290–306. https://doi.org/10.1111/j.1365-2486.2005.00903.x

Singh, M., Sarkar, B., Sarkar, S., Churchman, J., Bolan, N., Mandal, S., ... & Beerling, D. J. (2018). Stabilization of soil organic carbon as influenced by clay mineralogy. *Advances in agronomy*, *148*, 33-84. https://doi.org/10.1016/bs.agron.2017.11.001

Soethe, N., Lehmann, J., & Engels, C. (2007). Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. *Journal of Tropical Ecology*, *23*(3), 319–328. https://doi.org/10.1017/S0266467407004002

Sotta, E. D., Veldkamp, E., Guimarães, B. R., Paixão, R. K., Ruivo, M. L. P., & Almeida, S. S. (2006). Landscape and climatic controls on spatial and temporal variation in soil CO2 efflux in an Eastern Amazonian Rainforest, Caxiuanã, Brazil. *Forest Ecology and Management*, *237*(1–3), 57–64. https://doi.org/10.1016/j.foreco.2006.09.027

Strand, A. E., Pritchard, S. G., McCormack, M. L., Davis, M. A., & Oren, R. (2008). Irreconcilable Differences: Fine-Root Life Spans and Soil Carbon Persistence. *Science*, *319*(5862), 456–458. https://doi.org/10.1126/science.1151382

Tanner, E. V. J., Vitousek, P. M., & Cuevas, E. (1998). Experimental investigation of nutrient limitation of forests growth on wet tropical mountains. *Ecology*, *79*(1), 10–22.

Telles, E. de C. C., de Camargo, P. B., Martinelli, L. A., Trumbore, S. E., da Costa, E. S., Santos, J., … Oliveira, R. C. (2003). Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles*, *17*(2). https://doi.org/10.1029/2002GB001953

Ushio, M., Fujiki, Y., Hidaka, A., & Kitayama, K. (2015). Linkage of root physiology and

morphology as an adaptation to soil phosphorus impoverishment in tropical montane forests. *Functional Ecology*, *29*(9), 1235–1245. https://doi.org/10.1111/1365-2435.12424

Violita, V., Triadiati, T., Anas, I., & Miftahudin, M. (2016). Fine Root Production and Decomposition in Lowland Rainforest and Oil Palm Plantations in Sumatra, Indonesia. *HAYATI Journal of Biosciences*, 23(1), 7–12. https://doi.org/10.1016/j.hjb.2015.10.008

Vogt, K. A., Vogt, D. J., & Bloomfield, J. (1998). Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil*, *200*(1), 71–89. https://doi.org/10.1023/A:1004313515294

Wang, C., Chen, Z., Brunner, I., Zhang, Z., Zhu, X., Li, J., … Li, M.-H. (2018). Global patterns of dead fine root stocks in forest ecosystems. *Journal of Biogeography*, *45*(6), 1378–1394. https://doi.org/10.1111/jbi.13206

Wang, Y., Gao, G., Wang, N., Wang, Z., & Gu, J. (2019). Effects of morphology and stand structure on root biomass and length differed between absorptive and transport roots in temperate trees. *Plant and Soil*, *442*(1–2), 355–367. https://doi.org/10.1007/s11104-019-04206-7

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalised linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. I., Tanner, E. V. J., Sayer, E. J., … Corre, M. D. (2011). Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, *92*(8), 1616–1625. https://doi.org/10.1890/10-1558.1

Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., & Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecology*, *36*(4), 433–445. https://doi.org/10.1111/j.1442-9993.2010.02157.x

Yuan, Z. Y., & Chen, H. Y. H. (2010). Fine Root Biomass, Production, Turnover Rates, and Nutrient Contents in Boreal Forest Ecosystems in Relation to Species, Climate, Fertility, and Stand Age: Literature Review and Meta-Analyses. *Critical Reviews in Plant Sciences*, *29*(4), 204–221. https://doi.org/10.1080/07352689.2010.483579

Zimmermann, M., Meir, P., Bird, M. I., Malhi, Y., & Ccahuana, A. J. Q. (2009). Climate dependence of heterotrophic soil respiration from a soil- translocation experiment along a 3000 m tropical forest altitudinal gradient. European Journal of Soil Science, 60(6), 895– 906. https://doi.org/10.1111/j.1365- 2389.2009.01175.x

4.7 Supplementary material

Supplementary tables

Table S4.1. Loadings of the soil variables on the first four axes of the Principal Component Analysis (PCA) across the lowland forests and montane forests. Loadings in bold show the highest loading variables on each PC axis. EV is the error or proportion of variance.

Forest types	Soil properties	PC1 EV (0.39)	PC2 EV (0.26)	PC3 EV (0.16)	PC4 EV (0.09)
Lowland forests (Wet, Semi-deciduous, Deciduous)	Sand (%)	**0.41**	0.12		
	Silt (%)	-0.35	0.15	0.29	
	Clay (%)	-0.26	-0.33	-0.30	
	pH (H20)	-0.14	**0.47**		0.29
	N (%)	-0.27	-0.13	-0.44	0.25
	C:N ratio	0.34		-0.34	-0.225
	Total P (mg kg-1)	-0.20		**-0.52**	
	Total Al (mg kg-1)	-0.20	-0.43	0.19	
	Total Ca (mg kg-1)	-0.11	0.45	-0.26	0.28
	Total K (mg kg-1)	-0.21		0.37	**0.531**
	Total Mg (mg kg-1)	-0.28	0.39		-0.211
	Total Na (mg kg-1)	-0.27	0.17		-0.622
	CEC (mmol+kg-1)	-0.39	0.20		
Forest types	**Soil properties**	**PC1** EV (0.27)	**PC2** EV (0.27)	**PC3** EV (0.18)	**PC4** EV (0.10)
Montane forests (MTF)	Sand (%)	0.30	0.30	0.434	0.375
	Silt (%)	-0.37	0.27	-0.307	0.228
	Clay (%)	-0.13	-0.18	**-0.622**	0.313
	N (%)		**-0.58**		
	C:N ratio	0.12	-0.45	0.351	0.407
	Total P (mg kg-1)	**0.47**		-0.368	0.204
	Total Ca (mg kg-1)	0.42	0.28	-0.101	-0.403
	Total K (mg kg-1)	0.28	-0.43	-0.129	**-0.469**
	Total Mg (mg kg-1)	0.51		-0.202	0.344

Table S4.2. Generalised linear models (GAMs), for fine root carbon stock ($Cstock_{fr}$, Mg C ha^{-1}), productivity (NPP_{fr}, Mg C ha^{-1} yr^{-1}), residence time (RT_{fr}, yr), and fractional allocation of total net primary productivity to the fine roots ($Allocation_{fr}$). These are full models with all explanatory variables; for the best models (lowest AIC), see Table 4.2 in the main text. Explanatory variables: climatic variables of mean annual temperature (MAT, ^{o}C), mean annual precipitation (MAP, mm yr^{-1}), maximum cumulative water deficit (MCWD, mm yr^{-1}); soil properties of soil sand content (Sand, %), soil clay content (Clay, %), potassium (K, mg kg^{-1}), phosphorus (P, mg kg^{-1}), nitrogen (N, %), and potential hydrogen (pH H_2O, %). Standard error (SE), deviance explained (DE), root mean square error (RMSE), significance of the model coefficients P, and Akaike information criterion (AIC).

Forest types	Response variables	Explanatory variables	Estimate	SE	t-value	P	*DE*
Lowland forests (Wet, Semi-deciduous, Deciduous)	$Cstock_{fr}$	Intercept	-10.755838	9.941908	-1.081869	0.304709	40.30%
		Sand (%)	-0.006521	0.012964	-0.502988	0.625865	
		pH H2O (%)	-0.950853	0.64953	-1.463909	0.173933	
		P (mg kg-1)	0.001132	0.00172	0.658315	0.525201	
		K (mg kg-1)	-0.019095	0.014831	-1.287522	0.226911	
		MAP (mm yr-1)	0.000595	0.001271	0.467894	0.649891	
		MCWD (mm yr-1)	-0.026373	0.021382	-1.233433	0.24562	
		MAT (oC)	0.550572	0.389014	1.415302	0.187359	
	NPP_{fr}	Intercept	-6.707921	5.51791	-1.215663	0.252032	63.30%
		Sand (%)	0.010094	0.007195	1.402907	0.190921	
		pH H2O (%)	-0.259644	0.360499	-0.720235	0.487874	
		P (mg kg-1)	0.000556	0.000954	0.582296	0.573261	
		K (mg kg-1)	-0.014388	0.008231	-1.74796	0.111047	
		MAP (mm yr-1)	0.000294	0.000705	0.416464	0.685869	
		MCWD (mm yr-1)	-0.008777	0.011867	-0.739633	0.476527	
		MAT (oC)	0.28322	0.215908	1.311759	0.218917	
	RT_{fr}	Intercept	-3.997059	5.671476	-0.704765	0.497042	63.10%
		Sand (%)	-0.015439	0.007395	-2.087702	0.063373	
		pH H2O (%)	-0.748105	0.370532	-2.019004	0.071098	
		P (mg kg-1)	0.000628	0.000981	0.64055	0.536217	
		K (mg kg-1)	-0.001551	0.00846	-0.183325	0.858206	
		MAP (mm yr-1)	0.000351	0.000725	0.484397	0.638538	
		MCWD (mm yr-1)	-0.018485	0.012198	-1.515491	0.1606	
		MAT (oC)	0.258979	0.221917	1.167007	0.270282	
	$Allocation_{fr}$	Intercept	-8.737927	4.673503	-1.869674	0.061529	82.40%
		Sand (%)	0.017184	0.005967	2.879814	0.003979	
		pH H2O (%)	-0.17667	0.289676	-0.609888	0.541936	
		P (mg kg-1)	0.000674	0.000847	0.796025	0.426018	
		K (mg kg-1)	-0.0056	0.006428	-0.871192	0.38365	
		MAP (mm yr-1)	-0.000453	0.000571	-0.792713	0.427945	
		MCWD (mm yr-1)	0.000771	0.009519	0.080989	0.935451	
		MAT (oC)	0.322139	0.18427	1.74819	0.080431	

Forest types	Response variables	Explanatory variables	Estimate	SE	t-value	P	*DE*
Montane forests (MTF)	$Cstock_{fr}$	Intercept	-0.921138	1.508604	-0.610589	0.603615	75.80%
		P (mg kg-1)	0.002043	0.00148	1.379661	0.301692	
		N (%)	0.448734	0.760032	0.590415	0.61474	
		Clay (%)	0.035614	0.032654	1.090654	0.389306	
		K (mg kg-1)	-0.006153	0.006077	-1.012541	0.417853	
		MAP (mm yr-1)	-0.000233	0.000231	-1.009813	0.418891	
		MCWD (mm yr-1)	-0.005085	0.004925	-1.032327	0.410407	
		MAT (oC)	-0.034578	0.067511	-0.512184	0.659476	
	NPP_{fr}	Intercept	1.097109	0.785548	1.396617	0.297334	95.90%
		P (mg kg-1)	-0.001617	0.000771	-2.097549	0.170852	
		N (%)	-0.522719	0.395757	-1.320806	0.317441	
		Clay (%)	-0.014078	0.017003	-0.827936	0.494774	
		K (mg kg-1)	0.006458	0.003165	2.040881	0.178052	
		MAP (mm yr-1)	0.000217	0.00012	1.799706	0.213715	
		MCWD (mm yr-1)	0.001038	0.002565	0.404774	0.724831	
		MAT (oC)	0.048321	0.035154	1.374553	0.30302	
	RT_{fr}	Intercept	-1.996152	1.572573	-1.269354	0.332035	90.60%
		P (mg kg-1)	0.003648	0.001543	2.363801	0.141856	
		N (%)	0.982511	0.792259	1.240139	0.340682	
		Clay (%)	0.04893	0.034038	1.437484	0.287147	
		K (mg kg-1)	-0.01252	0.006335	-1.976264	0.186772	
		MAP (mm yr-1)	-0.000461	0.000241	-1.914428	0.195664	
		MCWD (mm yr-1)	-0.005878	0.005134	-1.144936	0.37077	
		MAT (oC)	-0.080099	0.070374	-1.138185	0.373019	
	$Allocation_{fr}$	Intercept	-3.783656	0.011516	-328.550809	0	100%
		P (mg kg-1)	0.001303	0.00001	126.981978	0	
		N (%)	1.241136	0.003757	330.313994	0	
		Clay (%)	-0.03193	0.000162	-197.536313	0	
		K (mg kg-1)	-0.014308	0.000066	-216.426463	0	
		MAP (mm yr-1)	-0.001339	0.000004	-309.091954	0	
		MCWD (mm yr-1)	0.167994	0.000508	330.440093	0	
		MAT (oC)	0.496645	0.001215	408.868253	0	

Supplementary figures

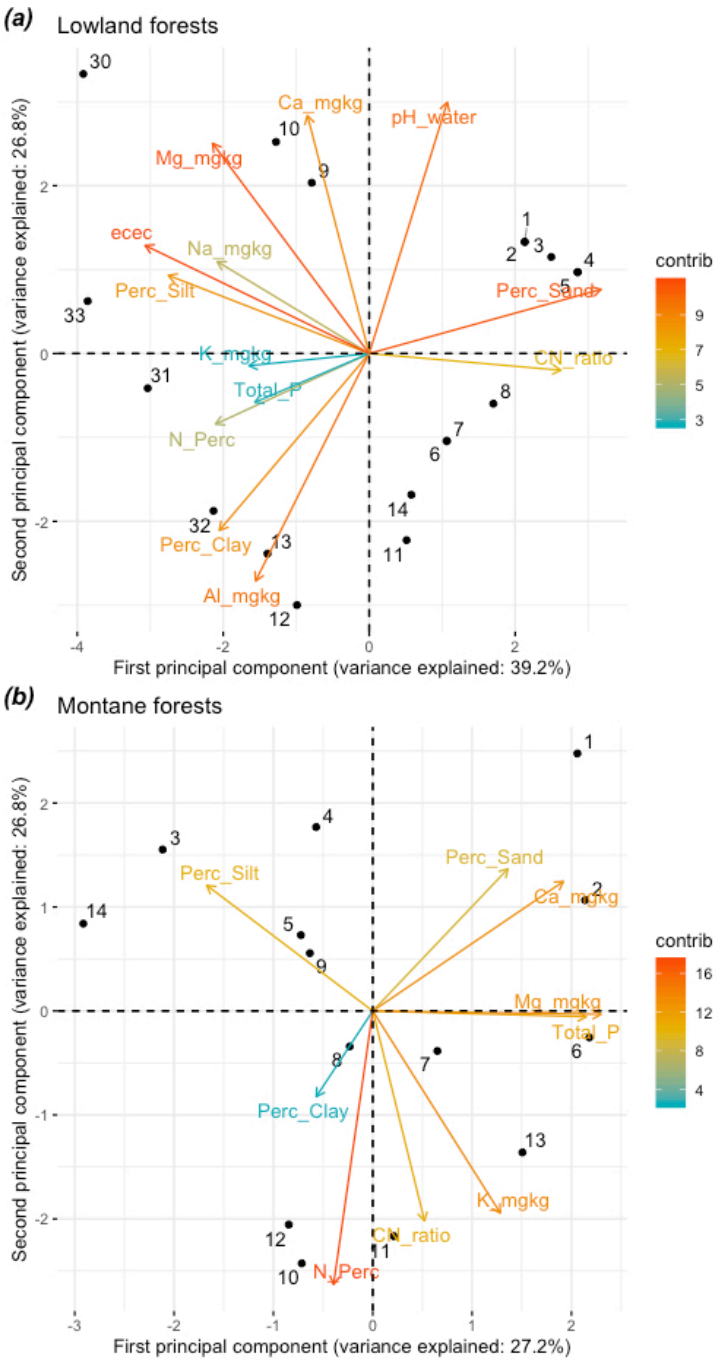


Figure S4.1. Principal Component Analysis (PCA) of plot-level soil properties across the lowland tropical forest types (a) and montane tropical forests (b).

Chapter 5: Vertical and temporal variation of fine root dynamics in Amazonian and Andean forests

In the previous chapter I quantified fine root dynamics and examined how soil properties and climate influence them at the pantropical scale. This paper is a more detailed analysis of root dynamics in one region, South America. Specifically, I examine the soil depth distribution and seasonal variation of fine root carbon stock and dynamics across nineteen plots from lowland Amazon to Andean montane forests. I also compare two techniques, ingrowth cores and rhizotrons, and discuss their advantages and disadvantages. The rhizotron technique allowed the estimation of productivity and mortality at monthly intervals and by different soil depths. This paper quantifies the seasonal and vertical variation and explores how this variation is related to environmental factors in semi-deciduous, moist, lower montane, and upper montane forests.

The results in this chapter are the largest and longest-running root dynamics report with data collected over eight years in some lowland forests sites and over four years in montane forests. I conceived this paper together with my supervisors and lead on data processing, analysis and writing. I directly collected data in fifteen of the nineteen sites, and played a leading role in developing the protocol and training data collectors in the other sites. Other co-authors collected and provided data from the other field sites. This paper was submitted to *Soil Biology and Biochemistry* in April 2021.

Title: Vertical and temporal variation of fine root dynamics in Amazonian and Andean forests

Authors: Walter Huaraca Huasco[a*], Cécile A. J. Girardin[a], Terhi Riutta[a], Beisit L. Puma Vilca[b], Fernando Hancco Pacha[b], Judith M. Laupa Roman[b], Alejandro Araujo-Murakami[c], Renata Freitag[d], Darcy F. Galiano Cabrera[b], Mary L Ortiz de Orue[b], Luis M Alvarez Mayorga[b], Maria E. Ezquerra Condori[b], Rosy Mamani Tacusi[b], Liliana Durand Baca[e], Filio Farfán Amézquita[b], Javier E. Silva Espejo[f], Sami W. Rifai[g], Daniel B. Metcalfe[h], Christopher E. Doughty[i], Norma Salinas Revilla[j], Luiz E.O. Aragão[k], Beatriz S. Marimon[d], Ben H. Marimon Junior[d], Imma Oliveras[a], Patrick Meir[l], Oliver L. Phillips[m], Miles Silman[n], and Yadvinder Malhi[a]

Manuscript submitted in Soil Biology and Biochemistry

Affiliations:

* Author for correspondence: **Walter Huaraca Huasco (stwamayr@gmail.com)**

[a](Huaraca Huasco; Girardin; Riutta; Oliveras; Malhi) Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

[b](Hancco Pacha; Puma Vilca; Laupa Roman; Galiano Cabrera; Ortiz de Orue; Alvarez Mayorga; Ezquerra Condori; Mamani Tacusi; Farfán Amézquita) Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú

[c](Araujo Murakami) Museo de Historia Natural Noel Kempff Mercado Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565 Casilla Postal 2489, Santa Cruz, Santa Cruz, Bolivia

[d](Freitag, Marimon, Marimon Junior) Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, CEP 78690-000, Nova Xavantina, MT, Brazil

[e](Durand Baca) Universidad Nacional Federico Villarreal de Lima, Lima, Perú

[f](Silva Espejo) Departamento de Biología, Universidad de La Serena, La Serena, Chile

[g](Rifai) ARC Centre of Excellence for Climate Extremes, University of New South Wales, Sydney, NSW 2052, Australia

[h](Metcalfe) Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

[i](Doughty) School of Informatics, Computing and Cyber systems, Northern Arizona University, Flagstaff, AZ 860011-5640 USA

[j](Salinas Revilla) Pontificial Catholic University of Peru, Lima, Peru

[k](Aragão) Divisão de Sensoriamento Remoto-DIDSR, Instituto Nacional de Pesquisas Espaciais, São Jose dos Campos, São Paulo, Brazil

[l] (Meir) Research School of Biology, Australian National University, ACT 2602 Australia

[m](Phillips) School of Geography, University of Leeds, UK

[n](Siman) Department of Biology, Wake Forest University, Winston-Salem, NC 27106, USA

Abstract

Fine root dynamics are a key component of ecosystem productivity and the belowground carbon (C) cycle. They vary both seasonally and with soil depth and this variation is controlled by climatic variables and soil properties. However, the determinants of spatial and temporal variation in fine root dynamics remain poorly understood, especially in tropical forests. Here we examine the seasonal variation and vertical distribution of fine root carbon stock, productivity, mortality, and residence time, using a novel large dataset spanning nineteen plots from lowland rainforests to montane forests in the Amazon and Andes regions. Fine root productivity and mortality were monitored over several years using the rhizotron and ingrowth core techniques to a consistent protocol to understand monthly and quarterly variation in root dynamics. Fine root carbon stock, productivity, and mortality decreased with soil depth and the rate of decline was determined by the thickness of the soil organic layer. The decline of root productivity with soil depth was stronger in lowland and pre-montane than in upper montane forests. Root residence time increased with soil depth and at higher elevations, ranging from seven months in lowland forests to five years in upper montane forests. Root productivity peaked in the wet season in lowland forests, suggesting control by moisture supply. In montane forests, however, root productivity decreased in rainy months, suggesting that waterlogging effects drive seasonal patterns in wet montane forests. Fine root mortality increased in the dry season in both lowland and montane forests, and mortality showed a second seasonal peak in the wet season in montane forests. Hence root mortality increased in both very dry and very wet conditions. This study is the first detailed analysis on the seasonal variation of fine root productivity and mortality, and on the root dynamics by soil depth in lowland and montane tropical forests.

Keywords: Fine root carbon stock, net primary productivity, mortality, residence time, montane forests, lowland forests.

5.1 Introduction

Fine root carbon stock, productivity, mortality, and residence time are key features of the ecosystem carbon budget in tropical forests (Girardin et al., 2013; Malhi et al., 2017). Fine roots at different soil depths perform the crucial function of water and nutrient uptake. Thus, there is a great need to improve our understanding of root dynamics and functioning, and their relationship to soil properties and climate at regional and global scales. Nonetheless, fine root dynamics have rarely been systematically studied along gradients of contrasting environmental conditions, especially in the tropics. Fine root mortality, residence time, and fractional allocation of total net primary productivity to fine roots, in particular, have been overlooked, with most studies focussing on carbon stock or productivity.

Fine root biomass can be a significant component of belowground carbon stocks. Many studies have shown that fine root biomass decreases with soil depth, with the top 10 cm soil layer reported to hold between 30% and 40% of total fine root stock in lowland Amazon forests (Telles et al., 2003; Trumbore et al., 2006), and between 50% and 70% in tropical montane forests, where the soil organic layer tends to be thicker than in lowland forests (Girardin et al., 2013; Hertel et al., 2009; Soethe et al., 2006).

Fine root productivity is much less studied but also known to decrease with soil depth (Cordeiro et al., 2020; Ibrahima et al., 2010); over 60% of root productivity occurs within the top 30 cm in a moist Amazon forest (Cordeiro et al., 2020). However, how this depth profile varies with climate and soil conditions remains poorly described from lowland moist to dry forests, and from lowland to upper montane forests across different soil types. The ratio between root carbon stock and productivity is called *root residence time*, and can be considered the mean time an atom of carbon persists in live root biomass. It is the inverse of root turnover rate (Assefa et al. 2017; Friend et al., 2014). Root residence time and root carbon stock are the main features of soil organic carbon accumulation and nutrient cycling rates (Assefa et al.,

2017; Soethe et al., 2007). In a Central Amazon forest, root residence time increased linearly with soil depth down to 90 cm (Cordeiro et al., 2020). However, there is a general lack of information on the soil depth distribution of fine root residence time in lowland and montane tropical forests.

When considering seasonal variation in tropical systems, fine root productivity and mortality vary with soil water availability and monthly precipitation. Root productivity generally increases during the rainy season in lowland tropical forests (Chairungsee et al., 2013; Cordeiro et al., 2020; Green et al., 2005; Jiménez et al., 2020; Priess et al., 1999), and 82% of root productivity occurs in the wet season in tropical savannas (Chen et al., 2004). Root mortality, which represents an important source of soil organic matter content, has been reported to peak in both drier and wetter periods (Röderstein et al., 2005), while root productivity responds to changes in rainfall with a time lag (Jiménez et al., 2020). On multiannual timescales in a near-equilibrium forest, root mortality must equal root productivity; on seasonal timescales; however, mismatches between the timing of root growth and death lead to seasonal variation in fine root biomass. Taken together, the literature suggests that the vertical distribution of fine root residence and mortality in lowland and montane tropical forests is poorly understood, as is their seasonal variation.

Two common approaches to assessing root dynamics are ingrowth cores and minirhizotrons. Ingrowth cores have the advantage of providing a direct volume-based assessment of root productivity, but introduce substantial disturbance at set-up when roots are removed from soils; hence roots grow in artificially disturbed and root-free soil, also root growth is strongly influenced by decomposition (Addo-Danso et al., 2016; Katayama et al., 2019). Minirhizotrons offer an alternative approach with little disturbance but small sample volume. Screen rhizotrons (Metcalfe et al., 2007) sample over a larger cross-section but a modest level of disturbance at the time of installation.

Here, we present an analysis of vertical and seasonal variation of root dynamics from a long-term study of tropical forest root dynamics, spanning an elevation gradient of over 3500 m, from dry lowland Amazon forests to tree line montane forests of the Andes. This unique dataset allows us to explore the factors driving the variation in fine root dynamics (productivity, mortality, and residence time) with soil depth; and to compare the seasonal variation in fine root productivity and mortality against precipitation patterns across Amazon and Andes forests. Specifically, we ask the following questions:

(Q1) How does the screen rhizotron technique compare with the ingrowth core technique for quantifying fine root productivity?

(Q2) How do fine root dynamics (productivity, mortality, and residence time) vary with soil depth and what soil factors determine this variation?

(Q3) How does fine root productivity and mortality vary seasonally and how is this variation related to environmental factors?

5.2 Materials and methods

5.2.1 Study site description

This study was carried out in tropical lowland and montane rainforest ecosystems in the Amazon-Andes region in South America, and the study areas are located in three countries: Bolivia, Brazil, and Peru (Table 5.1). The sites span a large-scale moisture transect in lowland South Amazonia from moist, to semi-deciduous, and deciduous forests from southern Peru to southern Brazil and an elevation transect of lowland to montane forest ecosystems that range between 595 m and 1000 m (pre-montane), 1527 m and 2020 m (lower montane), and 2758 m and 3537 m (upper montane) elevations. Nineteen one-hectare permanent plots were set up in different years by Amazon Forest Inventory Network (RAINFOR), Andes Biodiversity and Ecosystem Research Group (ABERG), and by Global Ecosystem Monitoring Network (GEM). This research was part of an intensive monitoring carbon cycle and functional traits projects

that was carried out by GEM network (Malhi et al., 2021) from 2009 to 2017, that encompassed many aspects of the carbon cycle including NPP, respiration and vegetation traits. The observation period varied across nineteen sites (n = 19), see Table 5.1.

Three lowland moist plots are located in Tambopata National Reserve of Madre Dios Region, Peru. In TAM-05 and TAM-06 plots monitoring started in 2005 (Aragão et al., 2009), and an additional plot, TAM-09, was set up in 2011(Bahar et al., 2017). In 2009, two plots were installed in semi-deciduous forests at the Hacienda Kenia (KEN-01, KEN-01) in Guarayos Province, Santa Cruz, Bolivia. The KEN-01 plot is located on deeper soils and in a slight topographic depression, but KEN-02 is located on shallow soils (less than 1 m depth) and hence has less available water (Araujo-Murakami et al., 2014; Doughty et al., 2015). In 2014, two plots were set up in Nova Xavantina (NXV-01, NXV-02) savanna (cerrado) and forest-savanna transition (cerradao) near the Bacaba Municipality Reserve, Brazil, and they are located on shallow and rocky soils (Gvozdevaite et al., 2018; Peixoto et al., 2017). The core region in our study is an Andes-Amazon elevation gradient in SE Peru (Malhi et al., 2017, 2010). Over 2006 - 2008, data were collected in seven montane and pre-montane plots (TON-01, SPD-02, TRU-08, TRU-07, TRU-04, TRU-03, WAY-01) in and near the Kosñipata Valley (Girardin et al., 2010). Over 2009 - 2011, seven plots (WAY-01, ESP-01, SPD-01, SPD-02, TAM-05, TAM-06 and TAM-09) were monitored for carbon cycle dynamics (Girardin et al., 2014; Huaraca Huasco et al., 2014; Malhi et al., 2014). In 2013, three new plots were set up, one in Acjanaco treeline forest (ACJ-01) of Manu National Park in upper montane forest (3537 m), the other two in pre-montane forests in the Pantiacolla (PAN-02, PAN-03) front range of the Andes located at 595 and 848 m, as a part of the largest plant functional traits campaign project (CHAMBASA; Challenging Attempt to Measure Biotic Attributes along the Slopes of the Andes) along different elevations (Blonder et al., 2018; Goldsmith et al., 2017; Malhi et al., 2017). The lower montane and upper montane forests are separated by the cloud immersion

base located near 1600 m (Girardin et al., 2010; Rapp et al., 2012).

5.2.2 Climate and soil variables

Mean annual temperature (MAT), precipitation (MAP), and solar radiation (SR) were recorded every 30 minutes using automatic weather stations installed in clearings close to the plots. Every month we also manually recorded soil temperature (Testo 926 thermometer) at 10 cm soil depth and volumetric soil water content (CS616 water content reflectometer) down to 20 cm (montane forests) and 10 cm (lowland forests) depth at each rhizotron and ingrowth core point. Soil data were collected and analysed following the RAINFOR protocol (Quesada et al., 2009) at the National Institute of Amazonian Research (INPA) soil laboratory in Manaus, Brazil (Table 5.1).

Table 5.1. Characteristics of 1ha permanent plots across different forest types of wet (WTF), deciduous (DTF), semi-deciduous (SDTF), pre-montane (PMTF), lower montane (LMFT), and upper montane tropical (UMTF) forests: elevation (Elevation, m asl), latitude (Lat., decimal degrees), longitude (Long., decimal degrees), mean annual precipitation (MAP, mm yr^{-1}), mean annual temperature (MAT, ºC), solar radiation (SR, Gj m^{-2} yr^{-1}), and soil properties of soil sand, clay, and silt percentage content (%), total nitrogen (N, %), total carbon-nitrogen ratio (C:N), total phosphorus (P, mg kg^{-1}), total potassium (K, mg kg^{-1}), and soil cation exchange capacity (CEC, mmol+kg^{-1}).

Country	Forest type	Site	Plot code	Soil type	Obs. period	Elev.	Lat.	Long.	MAP	MAT	SR	Sand	Silt	Clay	N	C:N	P	K
Brazil	DTF	Nova	NXV-01	Ferrasols	2014-2016	312	-14.70	-52.35	1530	25.20	NA	85.50	3.40	11.10	0.10	NA	107.50	39.90
		Xavantina	NXV-02	Ferrasols	2014-2016	324	-14.71	-52.35	1530	25.20	NA	75.30	6.90	17.80	0.10	NA	129.50	46.50
Boliva	SDTF	Kenia	KEN-01	Cambisols	2009-2017	384	-16.02	-62.73	1310	24.20	5.90	58.05	22.82	19.13	0.22	10.91	447.10	126.60
			KEN-02	Cambisols	2009-2017	384	-16.01	-62.74	1310	24.20	5.90	55.48	26.27	18.25	0.17	11.76	244.70	84.40
Peru	WTF	Tambopata	TAM-05	Cambisols	2006-2017	223	-12.83	-69.27	2545	24.40	4.80	40.00	17.00	44.00	0.16	9.44	256.30	35.10
			TAM-06	Alisols	2006-2017	215	-12.84	-69.30	2545	24.40	4.80	2.00	52.00	46.00	0.17	7.06	528.80	58.50
			TAM-09	Alisols	2006-2017	219	-12.83	-69.27	2545	24.40	4.80	NA	NA	NA	NA	NA	NA	NA
	Pre-MTF	Pantiacolla	PAN-02	Cambisols	2013-2014	595	-12.65	-71.26	2366	23.50	3.82	17.65	37.95	44.40	0.34	10.60	709.00	16.65
			PAN-03	Plinthosol	2013-2014	848	-12.64	-71.27	2835	21.90	3.82	44.95	22.65	32.40	0.22	11.30	1174.80	14.43
		Tono	TON-01	Cambisols	2007-2008	1000	-12.96	-71.57	3087	20.70	NA	27.83	32.42	39.75	0.42	12.22	751.00	154.26
	Lower-MTF	San	SPD-02	Cambisols	2009-2013	1527	-13.05	-71.54	5302	18.80	4.08	37.51	17.79	44.71	0.88	14.93	1630.71	154.36
		Pedro	SPD-01	Cambisols	2009-2013	1776	-13.05	-71.54	5302	17.40	4.36	31.35	26.97	41.68	1.19	18.01	1071.14	41.79
		Trocha	TRU-08	Cambisols	2007-2008	1885	-13.07	-71.56	2472	18.00	3.96	70.01	20.99	9.00	1.23	21.17	562.83	95.90
		Union	TRU-07	Cambisols	2007-2008	2020	-13.07	-71.56	1827	17.40	3.96	57.21	26.29	16.50	0.81	17.79	495.97	64.10
	Upper-MTF	Trocha	TRU-04	Umbrisol	2013-2014	2758	-13.11	-71.59	2318	13.50	3.32	13.61	12.50	73.89	1.99	15.47	746.76	182.31
		Union	TRU-03	Umbrisol	2007-2008	3044	-13.11	-71.60	1776	11.80	4.16	0.00	0.00	0.00	1.55	16.76	787.31	246.41
		Esperanza	ESP-01	Umbrisol	2009-2016	2863	-13.18	-71.59	1560	13.10	3.49	1.37	40.00	58.63	1.48	18.82	980.82	238.10
		Wayqecha	WAY-01	Umbrisol	2009-2016	3045	-13.19	-71.59	1560	11.80	3.51	43.65	16.50	39.85	0.88	21.23	1413.59	222.26
		Acjanaco	ACJ-01	Umbrisol	2013-2014	3537	-13.15	-71.63	1980	9.00	4.23	4.13	56.77	39.10	0.94	12.83	586.93	23.52

5.2.3 Fine root dynamics measurements

We used the fine root dynamics monitoring protocols developed by the RAINFOR-GEM network (Marthews et al., 2014; Metcalfe et al., 2009), using both the rhizotron and ingrowth core techniques. The methods are described in more detail in the GEM field manual (Marthews et al. 2014, available at gem.tropical forests.ox.ac.uk). We quantified the total fine root carbon stock, productivity, mortality, residence time, and fractional allocation of total net primary productivity to fine roots (≤ 2 mm diameter), down to 30 cm soil depth.

Fine root carbon stock ($Cstock_{fr}$) was estimated from the soil core samples at the initial installation of rhizotrons and ingrowth cores. A post hole digger shovel was used to collect soil core samples, with 12 cm diameter and 30 cm length, to assess vertical distribution of fine roots by 10 cm layers at each rhizotron point in two lowland (TAM-05, TAM-06), two premontane (PAN-02, PAN-03), and one upper montane cloud (ACJ-01) forest plots. In addition, at each ingrowth core point we recorded the total fine root carbon stock down to 30 cm depth by organic and mineral layer thickness, using the same soil core technique and size.

Fine root productivity (NPP_{fr_rh}) and mortality ($Mortality_{fr\text{-}rh}$) were recorded monthly using a screen rhizotron approach, using A4-size perspex screens (root windows) supported with wooden and metallic frames (Figure 5.1a). The rhizotron technique allows for monitoring at high temporal resolution (typically monthly) and provides a direct record of the appearance and disappearance of roots of different sizes at different depths, based on which we can estimate root productivity, mortality and residence time, and their seasonal dynamics and vertical distribution (Chairungsee et al., 2013; Green et al., 2005). However, there are some disadvantages of this technique. The soil may lose contact with the screen due to soil compression, and both the tracing the roots in the field and the data processing is time consuming (Girardin et al., 2013; Metcalfe et al., 2007). Furthermore, the conversion of the

two-dimensional rhizotron data into estimates of root mass per unit volume involves several assumptions (Marthews et al., 2014).

Nine screen rhizotrons (five in the TRU-07 plot) with a screen size of 21.0 cm width and 29.7 cm height were installed down to 30 cm depth in each plot, in a 30 m by 30 m regular grid. During installation the separation of the soil into organic and mineral layers was maintained in all removed and replaced soil material. The rhizotron screen was divided into three depth layers, 0-10, 10-20 and 20-30 cm, to examine the vertical pattern in root productivity, mortality, and residence time. Visible roots were traced with four colour permanent markers on transparent A4 acetate sheets placed over the rhizotron screen every month. Roots were colour coded by diameter class (≤ 1 mm = black, 1–2 mm = red, 2–3 mm = blue, ≥ 4 mm = green) and the dates of root appearance and disappearance were recorded by numbering each root increment traced (Figure 5.1b). Roots were recorded as alive at their first appearance, and then in future sessions, if not found, they were considered dead. Fine root productivity and mortality were estimated following the approach described by Girardin et al. (2013) and Metcalfe et al. (2007), using the equations below (1, 2) described by Bernier & Robitaille (2004) and Metcalfe et al. (2007). We used rhizotron-derived productivity data from all sites (n=19), but due to the time lag in mortality after the rhizotron installation, we used mortality data only from the sites where the observation period was >12 months (n=9; Table 5.1, Table 5.2), which we consider more robust (Supplementary Information).

$$\mathrm{XSr} = \frac{(3.1416)^2 \Sigma \mathrm{r}^2}{\sqrt{2}} \quad (1)$$

Where r is the mean root radius for each root diameter class: 0.25 (< 1 mm) and 0.75 (1-2 mm). Fine root productivity (Pr) and mortality (Mr) ≤ 2 mm were calculated using equation 2.

$$Pr(Mr) = 2 * 10^4 * Dfr * (1 - Fc) * XSr * \frac{sin\alpha * cos\gamma}{W} \quad (2)$$

Where Fc is the soil coarse fraction of particles > 2 mm and usually is zero in forest soils, Dfr is fine root tissue density (g mm^{-3}), α is the angle of rhizotron screen observation to the ground and that was inserted vertically (90^o), γ is the ground slope, W is the thickness of the rhizotron screen (usually was 4 mm), and 2 was a multiplication factor because the equal amount of roots would be expected to intersect from in front of the screen. The 10^4 is the value that converts square millimetre ground area into one hectare and grams into megagrams (Girardin et al., 2013; Metcalfe et al., 2007).

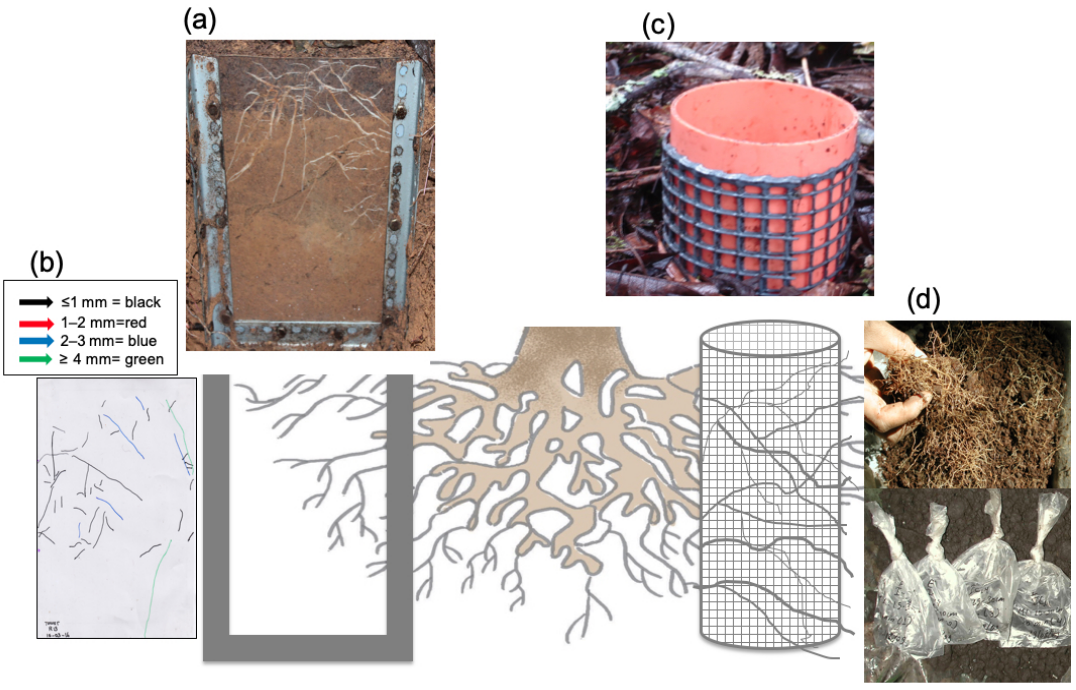


Figure 5.1. (a) Metallic rhizotron installed down to 30 cm soil depth, (b) roots traced on a transparent A4 acetate sheet with permanent markers, different colours corresponding to different fine root diameter classes, (c) an ingrowth core made of plastic-coated wire mesh installed down to 30 cm soil depth, and (d) fine root samples collected from the ingrowth core during 40 minutes.

Fine root productivity (NPP_{fr_ic}) was also measured every three months using the ingrowth core technique (Metcalfe et al., 2007; Vogt et al., 1998). Root ingrowth cores provide a direct, mass-based estimate of fine root productivity, and the samples can be analysed for root physical and chemical traits. However, ingrowth cores do not provide an estimate of fine root mortality or a direct estimate of residence time and they are not suited to monitoring root dynamics at high temporal resolution. The time between installation and removal, typically three months, is a compromise between ensuring that a sufficient mass of new roots has accumulated and minimising the mass loss due to root decay, which may lead to an underestimate of 25% in root productivity (Katayama et al., 2019). By requiring that soils are root-free at the point of installation, ingrowth cores also introduce substantial soil disturbance at the time of installation. Plastic cylindrical ingrowth cores were made with a diameter of 12 cm, length of 40 cm, and mesh size of 1.5 cm, which allows the regrowth of fine roots and movement of other soil organisms into the soil cores while keeping the core intact (Figure 5.1c). Sixteen ingrowth cores were installed down to 30 cm depth in each plot, in a 20 m by 20 m regular grid in fifteen plots (ACJ-01, ESP-01,KEN-01, KEN-02, NXV-01, NXV-02, PAN-02, PAN-03, WAY-01, SPD-01, SPD-02, TAM-05, TAM-06, TAM-09, and TRU-04), nine cores were installed in three plots (TON-01, TRU-8, TRU-03), and five in one plot (TRU-07). These latter plots were early installations prior to the full sampling protocol being established. The separation of the soil into organic and mineral layers was maintained as carefully as possible at the first installation and at each retrieval.

At the installation and every three months thereafter, fine roots in each ingrowth core were removed by hand search and the root-free soil was returned to the core until next retrieval. Roots were searched for 4 × 10-minute periods, with the samples from each time step kept separate (Figure 5.1d). Roots were rinsed in water, using sieves, to remove soil particles and then oven-dried at 70 ºC until constant mass and weighed to the nearest 0.01 g. Total fine roots

mass in each core was estimated by fitting a cumulative root mass over time curve to the 4 × 10-minute observations, and extrapolating to 120 minutes (Marthews et al., 2014) to account for roots that remained in the core after the 40-minute search period. This correction increased the estimates by 34% on average. Roots were separated and weighed to determine the total fine root carbon stock. To assess the root carbon stock (Mg C ha^{-1}) and productivity (Mg C ha^{-1} yr^{-1}), dry mass was converted into carbon units by assuming a carbon content of 45%. This value was determined by using the Fine-Root Ecology Database (FRED; roots.ornl.gov; Iversen et al., 2017) and calculating the mean fine root carbon content of broadleaved species (Huaraca Huasco et al., 2021). We express root stock and productivity in units of carbon, rather than dry mass, to be consistent with other studies published by the GEM network.

Fine root residence time (RT_{fr}) was assessed by dividing fine root carbon stock by fine root productivity (Assefa et al., 2017; Girardin et al., 2013), using both the ingrowth core data (all plots) and rhizotron data (five plots).

Fractional allocation of total NPP to fine roots ($Allocation_{fr}$) was calculated as fine root productivity (ingrowth core estimates) divided by total net primary productivity (NPP). The total NPP is the sum of root productivity (fine and coarse roots), canopy productivity (from litterfall), and woody productivity (stem and coarse wood productivity of stem ≥ 10 cm diameter). The total NPP for each plot has been published in previous studies (Araujo-Murakami et al., 2014; Girardin et al., 2010; Girardin et al., 2014; Huaraca Huasco et al., 2014; Malhi et al., 2017; Peixoto et al., 2017).

5.2.4 Statistical analyses

Fine root productivity estimates obtained using the rhizotron and ingrowth core techniques were compared with a Passing-Bablok non-parametric regression (Bilic-Zulle, 2011; Passing & Bablok, 1983) in the *mcr* package for the R software (Manuilova et al., 2015).

Vertical distribution of root dynamics, from top soil to 30 cm depth by 10 cm layers, was described by fitting a linear model with depth. To facilitate the comparison of the vertical pattern among sites with different total fine root productivity, we also fitted a linear model with depth and scaled productivity, where the root productivity of the topsoil layer was set to one. The slope of this relationship, which we refer to as 'the root productivity profile', describing how steeply productivity changes with depth, was then used in further analyses.

Generalised additive models (*mgcv* packages for R, Wood, 2019) were used to examine the relationships between root dynamics (C stock, productivity, mortality residence time, fractional allocation of total net primary productivity to the fine roots, productivity depth slope) and elevation, precipitation and soil properties. In the analysis of the seasonal pattern in root productivity and mortality, using monthly data, plot was included as a random effect. Other analyses used spatio-temporally averaged values (one estimate per plot) as response variables. All statistical analyses were conducted with R statistical software, version 3.6.0.

5.3 Results

5.3.1 Comparison of rhizotron and ingrowth core techniques

In lowland forests there was very good correspondence between ingrowth core (NPP_{fr_ic}) and rhizotron (NPP_{fr_rh}) measurements of root productivity, with the relationship not significantly different from the 1:1 line (Figure 5.2a), with an equal slope but fairly constant offset. On average, rhizotrons tended to give an 30% higher estimate of root productivity, with the percentage divergence being less in higher root productivity sites. In the montane sites, which tended to have deeper organic soil layers, there was more divergence between the methods (Figure 5.2b), with rhizotrons tending to yield 47% higher estimates, with the divergence being largely independent of root productivity.

Table 5.2. Mean and standard error of fine root carbon stock ($Cstock_{fr}$), productivity recorded with ingrowth cores (NPP_{fr_ic}) and rhizotrons (NPP_{fr_rh}), mortality recorded with rhizotrons, and residence time calculated from the ingrowth core estimates (RT_{fr_ic} = $Cstock_{fr}/NPP_{fr_ic}$) along the elevation gradient. Fine root mortality ($Mortality_{fr_rh}$) estimates in italics are based on short-term (one year) data, which we considered less reliable.

Forest type	plot code	Elevation (m)	$Cstock_{fr}$ mean ± SE Mg C ha^{-1}		NPP_{fr_ic} mean ± SE Mg C ha^{-1} yr^{-1}		NPP_{fr_rh} mean ± SE Mg C ha^{-1} yr^{-1}		Mortality mean ± SE Mg C ha^{-1} yr^{-1}		RT_{fr_ic} mean ± SE yr	
Deciduous	NXV-01	312	2.30	0.19	1.45	0.09	2.41	0.21	*0.20*	*0.04*	1.59	0.16
	NXV-02	324	1.59	0.18	1.94	0.16	2.15	0.17	*0.18*	*0.04*	0.82	0.12
Semi-deciduous	KEN-01	384	2.12	0.38	3.45	0.11	4.12	0.18	2.66	0.17	0.61	0.11
	KEN-02	385	2.57	0.46	2.68	0.06	3.48	0.16	2.03	0.13	0.96	0.17
Wet	TAM-06	215	1.50	0.10	1.11	0.04	1.59	0.05	1.02	0.03	1.36	0.10
	TAM-09	219	1.78	0.15	2.25	0.38	2.27	0.14	1.09	0.06	0.79	0.15
	TAM-05	223	2.36	0.14	1.89	0.07	2.57	0.07	1.52	0.04	1.25	0.09
Pre-montane	PAN-02	595	2.10	0.18	1.89	0.21	5.18	0.71	*0.89*	*0.12*	1.11	0.16
	PAN-03	848	4.20	0.41	0.99	0.13	3.91	0.42	*0.52*	*0.07*	4.25	0.68
	TON-01	1000	2.37	0.29	2.18	0.73	3.45	0.24	*2.39*	*0.21*	1.09	0.39
Lower montane	SPD-02	1527	3.12	0.34	1.26	0.09	2.34	0.09	1.62	0.08	2.48	0.33
	SPD-01	1776	3.73	0.30	1.49	0.07	2.82	0.12	1.17	0.06	2.51	0.23
	TRU-08	1885	5.95	0.59	2.93	0.16	6.79	0.37	*2.17*	*0.18*	2.03	0.23
	TRU-07	2020	6.25	0.94	1.62	0.16	5.52	0.43	*2.27*	*0.28*	3.85	0.70
Upper montane	TRU-04	2758	6.20	0.81	1.08	0.14	2.80	0.16	*0.46*	*0.06*	5.74	1.04
	ESP-01	2863	4.85	0.37	1.16	0.05	3.48	0.16	1.28	0.07	4.18	0.36
	TRU-03	3044	4.53	0.57	1.18	0.21	5.43	0.34	*2.20*	*0.18*	3.84	0.83
	WAY-01	3045	4.68	0.67	1.17	0.06	2.68	0.10	1.75	0.08	4.00	0.61
	ACJ-01	3537	2.81	0.30	0.97	0.27	2.12	0.17	*0.40*	*0.04*	2.89	0.86

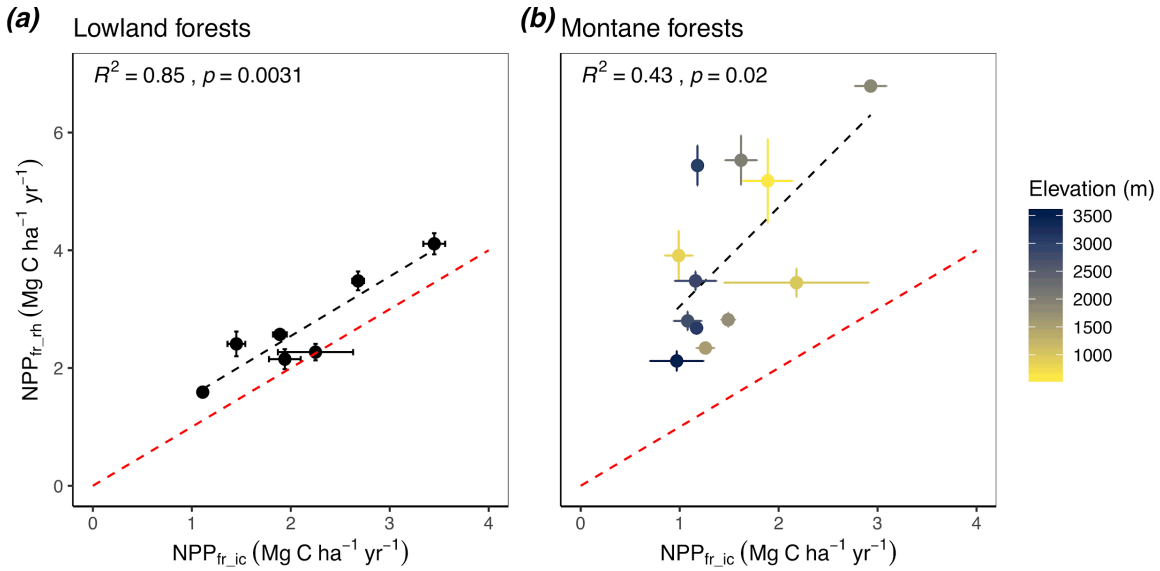


Figure 5.2. Comparison of fine root productivity estimates using ingrowth core (NPP_{fr_ic}) and rhizotron (NPP_{fr_rh}) techniques in (a) lowland forests (y = a + bx, where a = 0.70 ± 0.60, b = 0.98 ± 0.27) and (b) montane forests (a = -2.39 ± 2.93, b = 4.48 ± 2.65). The black dashed lines show the linear regression model, with the R^2 and p-values shown in the panels, and the dashed red line shows the 1:1 relationship.

5.3.2 Fine root carbon stock

Fine root carbon stock decreased with soil depth in most sites where the vertical gradient was measured (Figure 5.3a), but increased at higher elevations, matching increasing soil organic layer thickness (Figure 5.3b). We recorded a large variation in the vertical distribution of $Cstock_{fr}$ within the top 30 cm of soil at different elevations (Figure 5.3a). The mean proportion of root carbon stock by 10 cm soil layers was 56% (0-10 cm), 28% (10-20 cm), and 16% (20-30 cm) respectively in lowland forests. In two pre-montane forests, the corresponding values were 73%, 16%, and 11%, and in upper montane forests (3537 m) root density barely declined with depth (38%, 30%, and 32%) (Figure S5.1). Overall, fine root C stock had a positive, plateauing relationship with elevation, with the highest root carbon stock recorded at lower montane forest at 2020 m, and the lowest C stock in wet lowland forest at 215 m (Figure 5.3b). If examined separately by soil organic and mineral layers, fine root C stock in the organic layer showed a humped relationship with elevation, with peak C stock observed at 2020 m (mid-elevation), and C stock in the mineral layer showed a negative relationship with elevation.

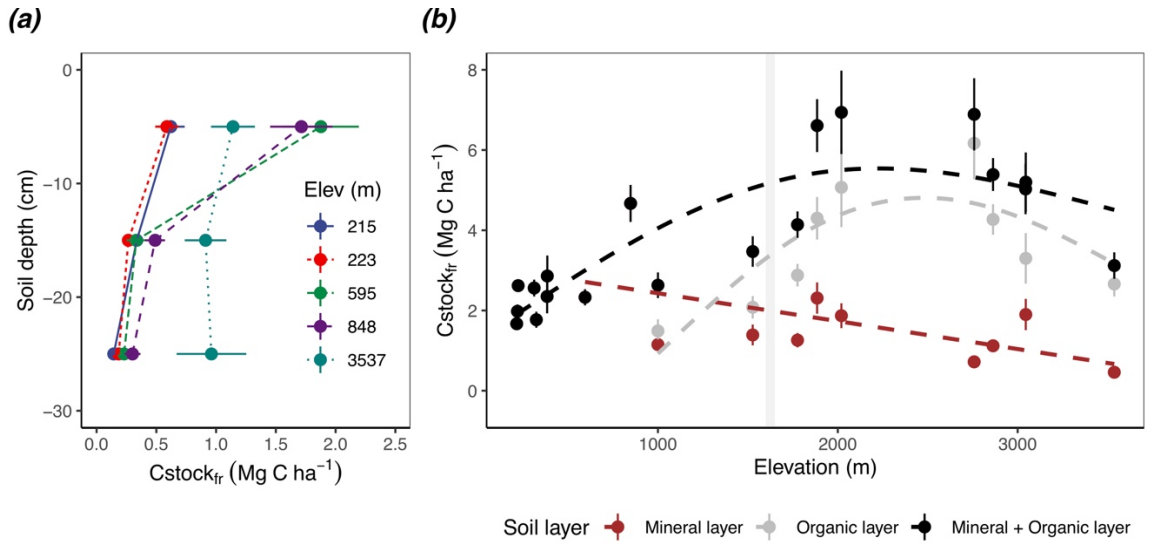


Figure 5.3. (a) Distribution of fine root (< 2mm) carbon stock (Cstock$_{fr}$, Mg C ha^{-1}) by 10 cm soil layers from 0 to 30 cm depth at five elevations. (b) Variation of total fine root C stock down to 30 cm soil depth (mineral and organic layers, black dots, $r^2 = 0.81$, $p < 0.001$), fine root C stock in the organic layer (grey, $r^2 = 0.66$, $p = 0.03$), and fine root C stock in the mineral layer (red, $r^2 = 0.27$, $p = 0.05$) along the elevation gradient from lowland to montane forests. The vertical grey area on panel b shows the cloud base zone (1600 m asl) in lower montane forests. The dashed lines show a generalised additive model fits to the data.

5.3.3 Fine root net primary productivity and fractional allocation of NPP to fine roots

Root productivity declined with soil depth across lowland wet, deciduous, pre-montane, three lower montane forests (1527 m, 1776 m, and 1885 m), and at three upper montane forests (2863 m, 3044 m, and 3045 m) (Figure 5.4). No linear relationships between root productivity and soil depth were observed in three montane forests of 2020 m, 2758 m, and 3537 m (Figure 5.4e-g). The mean proportion of NPP$_{fr_rh}$ by 10 cm soil depth was 42% (0-10 cm), 31% (10-20 cm), and 27% (20-30 cm) respectively for three lowland wet forests, and the highest proportion of fine root productivity in the top 10 cm of soil was recorded in a pre-montane forest (848 m) that decreased from 61% (0-10 cm), 26% (10-20 cm) to 13% (20-30 cm) (Figure S5.1).

The steepness of the NPP$_{fr_rh}$ decreased with increasing elevation, and also decreased with increasing soil organic layer thickness (Figure 5.5a-b). Steep root productivity profiles were observed in pre-montane and lower montane forests and shallow profiles were recorded

in upper montane forests with thick soil organic layers. The total annual root productivity recorded down to 30 cm with rhizotrons (NPP_{fr_rh}) increased with increasing elevation from lowland to above the cloud base immersion zone, and then decreased. On the other hand, fine root productivity recorded with ingrowth cores (NPP_{fr_ic}) showed a monotonic decrease with increasing elevation (Figure 5.5c). The highest annual fractional allocation of total NPP to fine roots was recorded at 1885 m (lower montane) and lowest was recorded at 215 m elevation (Figure 5.5d).

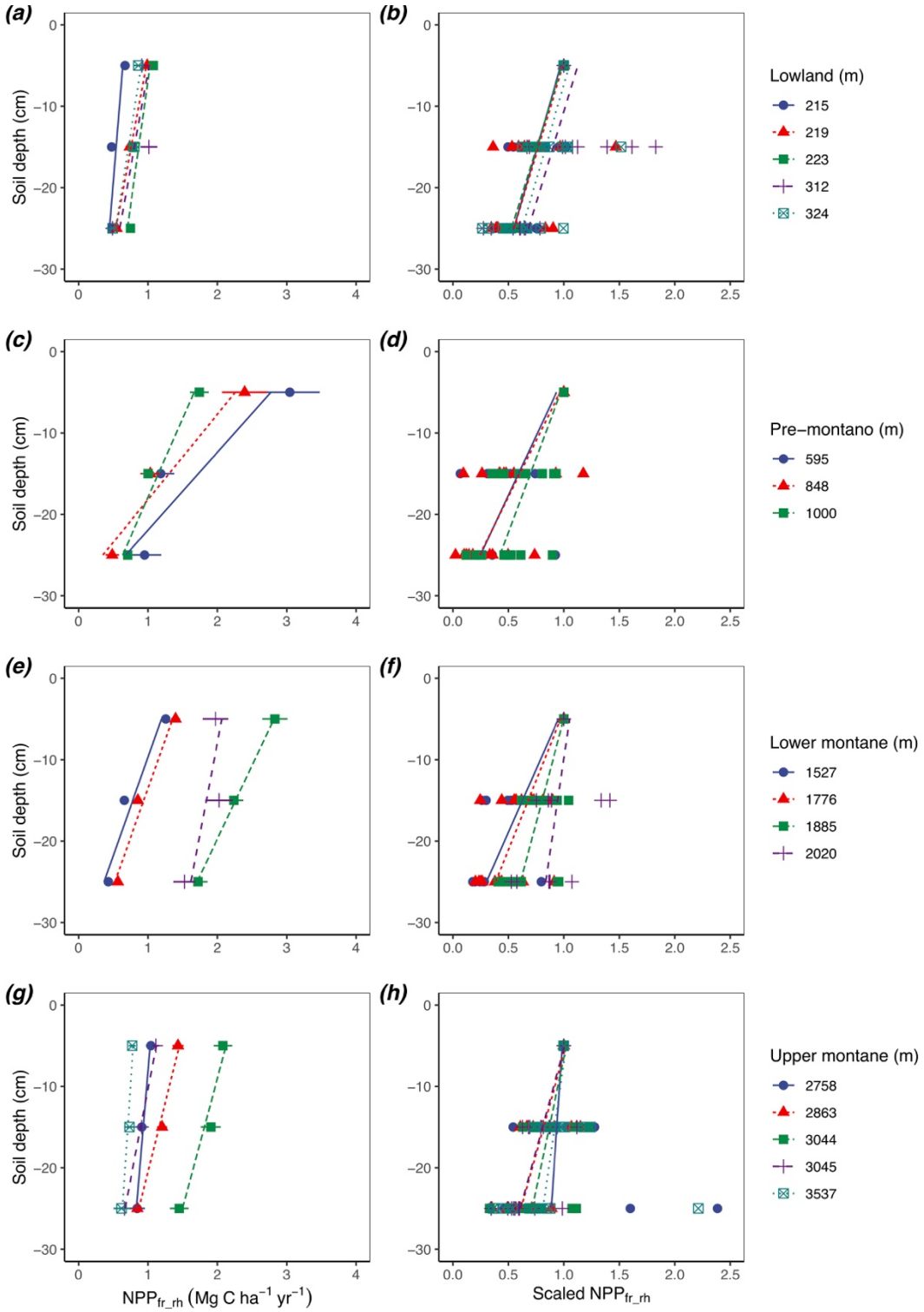


Figure 5.4. Vertical distribution of fine root productivity recorded with rhizotrons (NPP_{fr_rh}) by 10 cm soil layers from 0 to 30 cm depth, grouped by forest types and elevation (m asl). Left panels (a, c, e, g) show absolute values and right panels (b, d, f, h) show scaled values relative to the root productivity in the 0-10 cm layer.

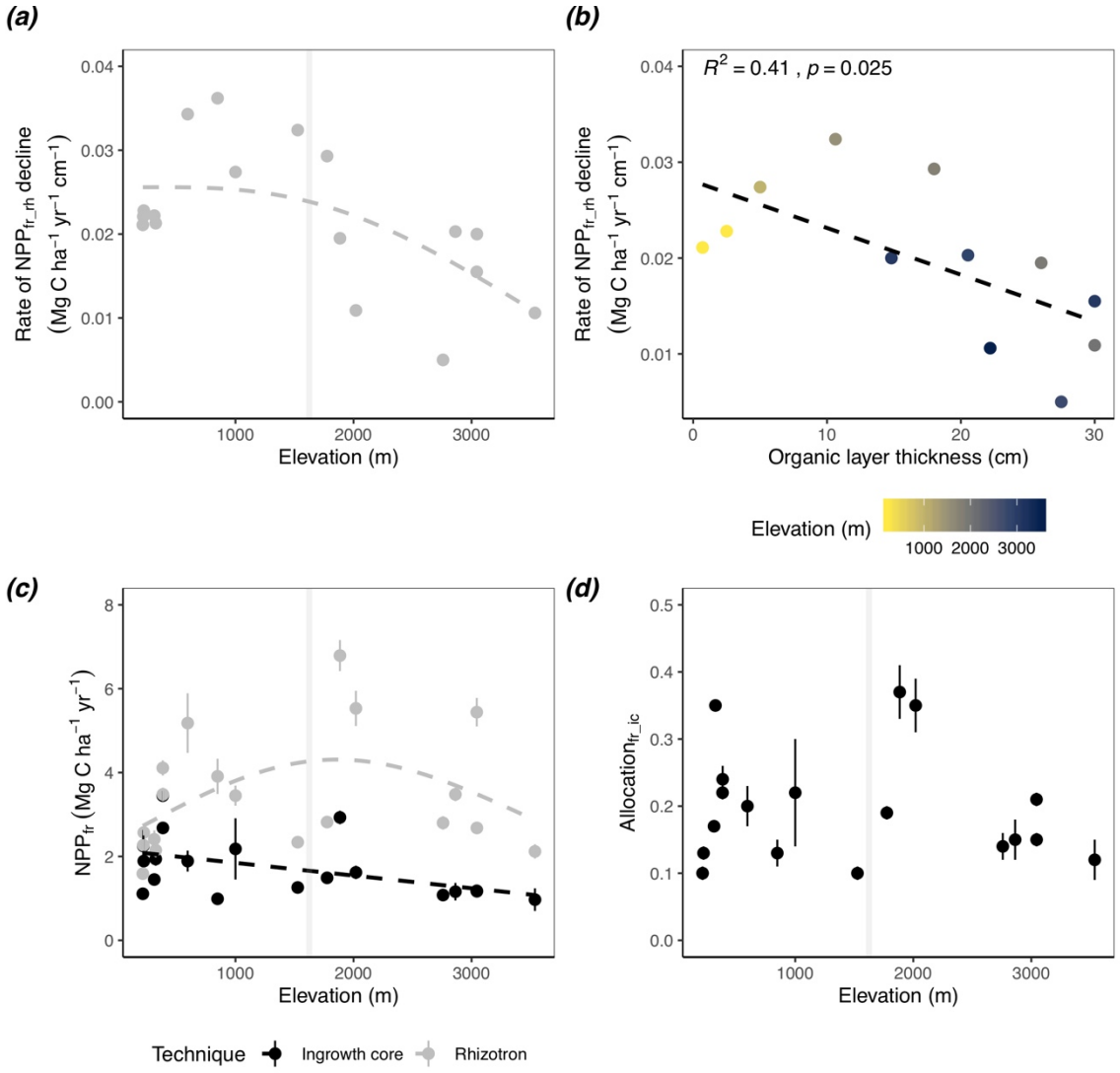


Figure 5.5. (a) The relationship between elevation and the steepness of the root productivity profile (the y axis values are negative slopes) ($r^2 = 0.20$, p = 0.0147) of the linear regression of scaled fine root productivity (NPP_{fr}) and soil depth (see Figure 5.4, right panels) using the rhizotron technique. (b) Linear relationship between organic layer thickness and the slope of the linear regression of scaled fine root net primary productivity (y = a + bx, where a = 0.028 ± 0.003, b = -0.000488 ± 0.00018x) by elevation (coloured dots). (c) The relationship between elevation and NPP_{fr} recorded with ingrowth core (black dots, $r^2 = 0.19$, p = 0.0129) and rhizotron (grey dots, no significant relationship) techniques, and (d) the relationship between elevation and carbon allocation to NPP_{fr} as a fraction of total NPP recorded using ingrowth core the technique. The vertical grey area on panel b shows the cloud base zone (1600 m asl) in lower montane forests. Dashed lines show generalised additive model fits where they are significant.

5.3.4 Fine root residence time

Fine root residence time increased with soil depth in montane forests (595 m, 848 m, and 3537 m), but decreased with soil depth in lowland forest (215 m and 223 m) (Figure 5.6a). RT_{fr_ic} increased with increasing elevation (Figure 5.6b). High variation of RT_{fr_ic} was observed along the elevation gradient; the highest RT_{fr_ic} was recorded in an upper montane forest (2758 m) and the lowest record was recorded in a semi-deciduous lowland forest (384 m). The mean RT_{fr_ic} was 2.39 ± 0.38 years across the elevation gradient, and the mean values for lowland, premontane, lower, and upper montane forests were 1.05 ± 0.13, 2.15 ± 0.41, 2.72 ± 0.37, and 4.13 ± 0.74 years respectively. Hence, mean root lifetime increased approximately fourfold with elevation.

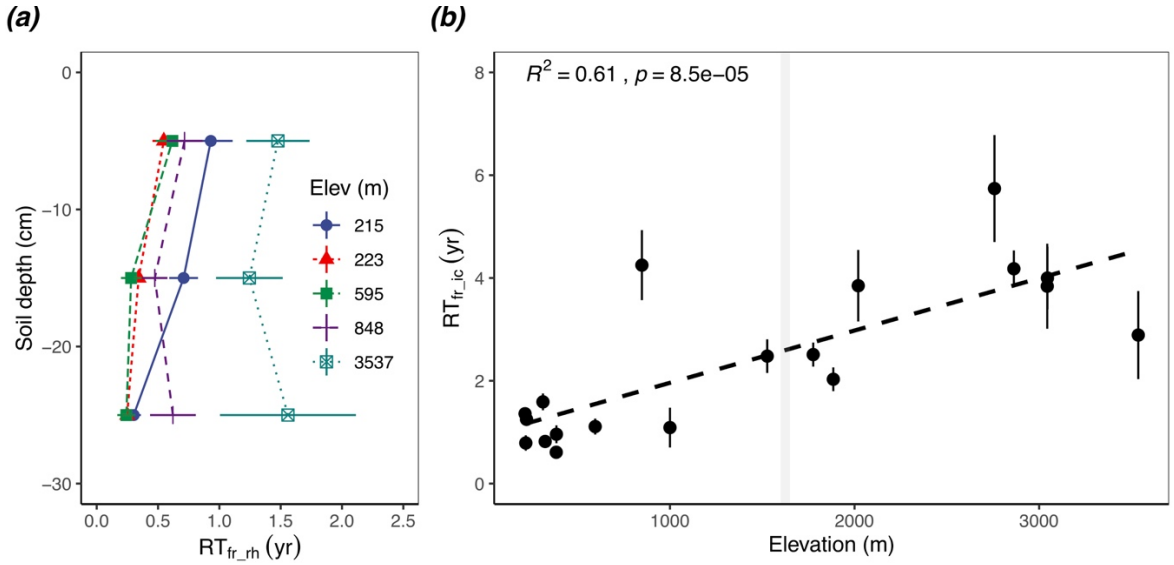


Figure 5.6. (a) Vertical distribution of fine root residence time recorded in five elevations (Elev, m) recorded with rhizotrons (RT_{fr_rh}). (b) The relationship between elevation and residence time, recorded down to 30 cm soil depth (dashed line is a linear fit: y = a ± bx, where a = 0.9431 ± 0.3609, b = 00102 ± 0.0001) recorded with ingrowth cores (RT_{fr_ic}). The vertical grey area on panel b shows the cloud base on lower montane forests.

5.3.5 Seasonal variation of net primary productivity and mortality of fine roots

Figure 5.7 shows the long-term seasonal variations of NPP_{fr_rh} and $Mortality_{fr_rh}$ recorded in five lowland forests (215 m, 219 m, 223 m, 384 m, 385 m) and four montane forests (1527 m, 1776 m, 2863 m, 3045 m); these are the only sites with consistent records of four years or more. In lowland moist forests (215 m, 219 m, and 223 m), we observed a clear response to precipitation patterns, with root mortality increasing during the dry season when root productivity is low, and productivity increasing at the start of the wet season. In lowland semi-deciduous forest (384 m, 385 m), we observed a dual peak in root mortality, at the start and at the end of the dry season (April and October), with lowest root productivity towards the end of the dry season (September and October).

In two lower montane forests, we observed the highest root productivity in July (early dry season) and the highest $Mortality_{fr_rh}$ in June (1527 m) and May (1776 m); the lowest root mortality was recorded at the beginning of the rainy season, in August. In upper montane forests, two peaks were recorded with high root productivity in June and December at 2863 m (humid forest) and May and December at 3045 m (treeline forest), while July and December were critical months for high mortality for both treeline forests.

In lowland forests, the difference between root mortality and productivity had a negative linear relationship with precipitation, which explained 27% of the variation (Figure 5.8a). However, in montane forests, there was no significant relationship with precipitation (Figure 5.8b). The combined analysis of lowland and montane forests showed that root mortality was highest under extreme wet and dry conditions: it increased with decreasing precipitation under 200 mm (dry months) and with increasing precipitation over 600 mm (rainy months) (Figure 5.8c). However, precipitation explained only 6% of the variation (marginally significant, $p=0.0508$) (Figure 5.8c).

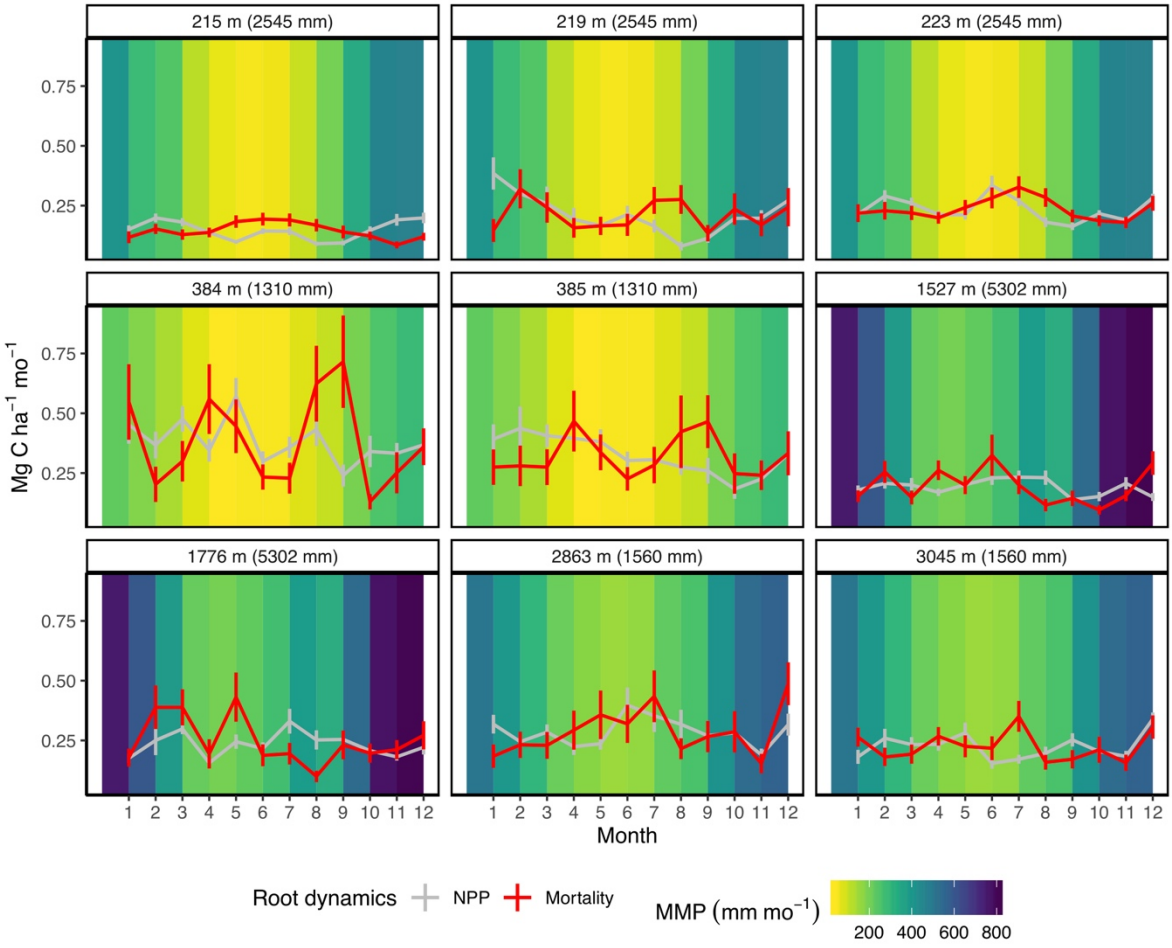


Figure 5.7. Seasonal variation (mean and standard error) of fine root productivity (NPP_{fr_rh}, grey) and mortality ($Mortality_{fr_rh}$, red) recorded with rhizotron technique in three evergreen lowland forests (215 m, 219 m, 223 m), two semi-deciduous lowland forests (384 m, 385 m), two lower montane forests (1527 m, 1776 m) and two upper montane forests (2865 m, 3045 m). The panel titles show the elevations (m) and mean annual precipitation (mm) of each site. The background colors show the monthly mean precipitation (MMP, mm mo^{-1}).

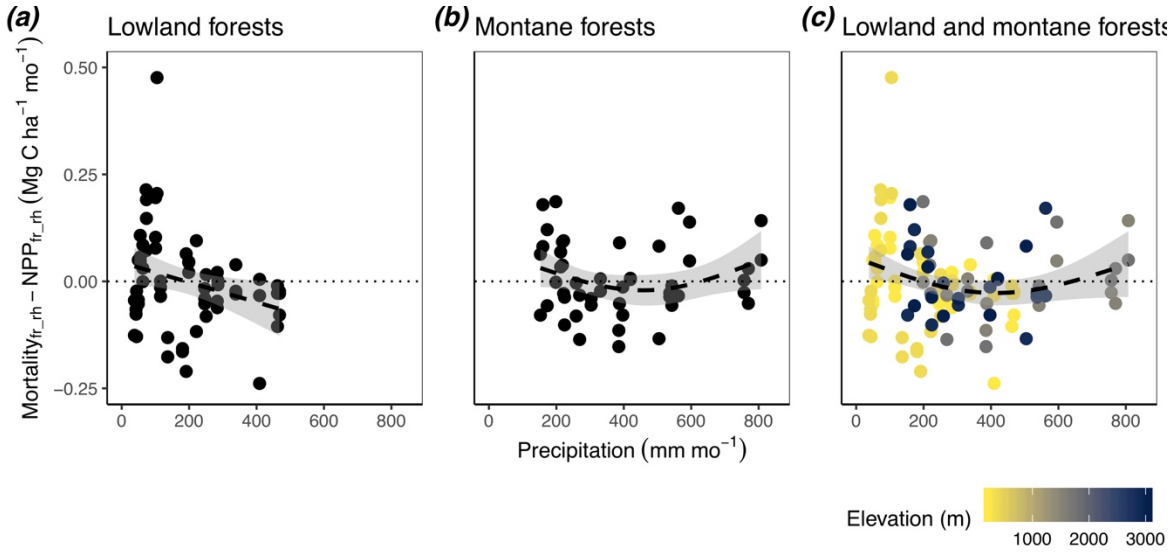


Figure 5.8. Generalised additive model predictions of the relationship between the monthly mean precipitation and the net monthly disequilibrium between fine root mortality and productivity (Mortality$_{fr_rh}$ - NPP$_{fr_rh}$, Mg C ha^{-1} mo^{-1}), recorded with rhizotrons, in (a) lowland forests (r^2 = 0.27, p = 0.0005), (b) montane forests (r^2 = 0.12, p = 0.105), and (c) across lowland and montane forests (data points coloured by elevation, r^2 = 0.06, p = 0.05). The thick dashed lines show the model fit, and the grey bands show the 95% confidence interval of the model predictions. The horizontal dotted line at zero indicates an equilibrium between monthly fine root mortality and productivity.

5.4 Discussion

5.4.1 Rhizotron and ingrowth approaches to monitoring root dynamics in tropical forests

This study provided an opportunity to compare two approaches to measuring fine root dynamics. Ingrowth cores have the advantage of providing a volume-based estimate of root productivity but have the disadvantage of introducing substantial disturbance and creating altered root growing conditions (disturbed, root-free soils). Screen rhizotrons have the advantage of sampling a large soil area (unlike conventional minirhizotrons) but also introduce a degree of artifice: they enable tracking of root mortality and detailed profile analysis and higher temporal resolution, but are substantially more labour-intensive. This study presents the largest comparison of ingrowth core and screen rhizotron techniques (Figure 5.1) across a range of tropical forest environments (Figure 5.2). The strong linear relationship between fine root

productivities recorded with the ingrowth core and rhizotron techniques across lowland forests increases confidence in the robustness of both approaches in these conditions, although there is a still a tendency for rhizotrons to produce higher estimates. This suggests either overestimation by rhizotron approaches, or underestimation by ingrowth cores. A paleotropical study reported that fine root productivity rates measured with ingrowth core techniques varied with the timing of sampling, and fine root decomposition between subsequent harvests of ingrowth cores may lead to underestimation root productivity by up to 25% (Katayama et al., 2019). The rhizotron approach allows for fine temporal sampling and hence less bias from root mortality. The rhizotron technique can therefore provide a better understanding of fine root phenology (Endo et al., 2019; Nakahata & Osawa, 2017; Van Do et al., 2016).

In montane forests with thick organic soils, there is greater divergence between the two approaches, with rhizotrons yielding consistently higher values than ingrowth cores. One possibility is that rhizotrons overestimate fine root productivity in waterlogged organics soils, for example if the presence of the rhizotron facilitates drainage in these frequently waterlogged soils. Compared to ingrowth cores, screen rhizotron technique causes minor disturbances of soil chemical and physical properties. Also, the local soil is disturbed only one time, during the rhizotron installation. In contrast, the other possibility is that ingrowth cores are consistently underestimating fine root productivity in montane soils. This may be because of the trimonthly impact of harvesting, processing and reinstalling ingrowth cores, leading to particularly high impacts in fragile montane soils. Moreover, in the dry season, these organic soils tend to contract and this can sometimes induce separation of the core from the surrounding soil matrix, breaking fine roots and preventing new root entry. In Ecuadorian montane forests, root productivity recorded with mini-rhizotron was found to be higher than with ingrowth cores in an upper montane forest with annual precipitation over 4500 mm (Moser et al., 2010). Hence,

the weight of arguments suggests that the rhizotrons may be giving more robust estimates of root productivity, especially in montane forests.

5.4.2 Variation of fine root dynamics with depth and elevation

This study provides new insights into tropical forest root dynamics by providing vertical profiles of productivity, mortality, and residence time through use of the screen rhizotron approach. Fine root productivity decreased with soil depth and the rate of root productivity declined with increasing elevation, with the highest productivity proportion being recorded in the top 10 cm soil depth in pre-montane forests. The steep decline in root productivity down to 30 cm soil depth in some pre-montane and lower montane forests is likely related to high soil nutrient availability in the litter and surface soil layers (Figure 5.5a) and to ensure a rapid nutrient capture before they are leached away (Table 5.1, Figure 5.5b). In tropical regions, there are few of studies reporting soil depth distribution of root productivity, but the few studies available show that fine root productivity is the highest in the first 10 cm soil depth in lowland and pre-montane forests (Cordeiro et al., 2020; Ibrahima et al., 2010). The root profile on organic soils was much less steep than on lowland mineral soils. This may be because organic soils are easy to penetrate so there is no cost to root exploration throughout the soil profile. Alternatively, the nutrient supply is less concentrated in the surface layer, because more of the organic material originates from root mortality, rather than from surface litter, and the slow decomposition rates in mountains means surface nutrients are not rapidly leached away. Hence root foraging throughout the 30 cm has equal cost and return in nutrients.

We found that fine root residence time decreased with soil depth in lowland and pre-montane forests, but showed litter change or even increased with depth in montane forests. In lowland forests, this suggests that the nutrient-sparse environment of deeper soils favours short-lifetime foraging roots that can explore a wider volume. In montane forests, the equivalence of nutrient supply and foraging cost at depth compared to the surface means there

is little pressure to reduce root lifetimes. The slight increase in root lifetime near the base of the organic layer may be associated with more regular moisture supply at the interface with the mineral layer.

In highly weathered and nutrient depleted soils of lowland terra firme Amazonian forest root residence time increased down to 90 cm depth (Cordeiro et al., 2020), and was 1.83 years down to 30 cm soil layer, which is higher than our values for lowland moist and semi-deciduous forests (Tambopata, Bolivia) that ranged between 0.61 and 1.39 years; these western Amazonian sites are generally more fertile than eastern Amazonian sites (Quesada et al., 2020). This suggests that root residence time in Amazon forests is related to soil properties: soil sand content and acidity (Huaraca Huasco et al., in press). Consistent to our findings for Amazonian forests, a fertilization experiment in lowland wet forests of Panama reported that four years of soil nutrient fertilization decreased root residence time (Yavitt et al., 2011). Also, some tropical old-growth forests can be sensitive to addition of N, which results in a decrease in fine root C stock (Zhu et al., 2013). Nitrogen has been shown to decrease with soil depth in tropical regions (Campos et al., 2017; Soethe et al., 2006) and this negative relationship between N and soil depth may be the reason why root residence time increases with soil depth.

Overall, root residence time increased with increasing elevation. Tropical montane forests studies have demonstrated that residence time is negatively to temperature and soil phosphorus content, and positively related to soil C:N ratio and N (Huaraca Huasco et al., in press; Okada et al., 2017; Sierra Cornejo et al., 2020). The long lifespan of fine roots in montane forests may be related to less fine root herbivory pressure (Galbraith et al., 2013). In addition, Sierra Cornejo et al. (2020) suggest that decreasing temperature in montane forests may favour plants to develop thick root sclerenchyma cell tissues as a protection trait from cold environments. This hypothesis remains to be tested with root anatomical trait studies across tropical montane forests at the level of tree species taxa.

5.4.3 Seasonal variation of fine root productivity and mortality

In lowland forests, fine root productivity increased with increasing monthly precipitation, while root mortality increased with decreasing precipitation. Previous seasonal variation studies of fine root productivity with ingrowth core technique across lowland Amazon regions have reported that fine root productivity increased during the rainy season (Araujo-Murakami et al., 2014; da Costa et al., 2014; Doughty et al., 2014; Malhi et al., 2014; Rocha et al., 2014). Furthermore, a soil irrigation experiment in a semi-deciduous lowland forest of Panama showed that fine root productivity increased with increasing soil water content (Cavelier et a., 1999). Therefore, there is consistent evidence from previous studies and ours on the importance of soil moisture and water availability on seasonal variation of fine root productivity across lowland tropical forest ecosystems. The higher fine root productivity recorded in the rainy season is probably linked to alleviation of moisture limitation. During the wet season, the decomposition of the organic matter accumulated during the dry season increases, releasing nutrients from the litter layer and other organic matter, which may stimulate root productivity. Monthly variation in fine root dynamics may also correlate with leaf flushing. July to October has been reported as the season of the highest leaf fall and August to October as the season of the peak leaf flush in lowland Amazonian forests (Araujo-Murakami et al., 2014; Malhi et al., 2014). However, we recorded a decrease in fine root productivity and highest mortality between August and September, suggesting there may be an allocation trade-off where carbon is invested in leaf flushing and away from roots.

In montane forests, two patterns of seasonal variation of fine root productivity and mortality were recorded (Figure 5.7, Figure 5.8). The first pattern was observed in lower montane forests, where root productivity increased in both rainy and dry seasons, and root mortality was higher than productivity in the rainy season. The second seasonal variation was reported in the upper montane and treeline forests where both root productivity and mortality

increased in the rainy and dry seasons (Figure 5.7). Röderstein et al. (2005) also reported that root mortality peaked during the driest and wettest seasons in Ecuadorian montane forests. The increased root mortality and decreased root productivity in the rainy season may be due to partial and total soil anoxia in these waterlogged organic soils. However, the increasing fine root productivity in the dry season may be a compensation effect to increased root mortality in the rainy season. Our finding is also supported by the difference between root mortality and productivity relationship with monthly precipitation (Figure 5.8); this relationship revealed that root mortality increased with high precipitation in montane forests. This may also indicate the high nutrient release in the rainy season with negative effects on root productivity and mortality increases due to high root herbivory. In addition, our findings support a previous finding that root productivity responded positively to annual solar radiation variation (Girardin et al., 2014; Huaraca Huasco et al., 2014), but root mortality responded negatively to increasing solar radiation at the beginning of austral summer. In tropical montane forests, the relationship between leaf fall productivity and root dynamics may be less straightforward. All these relationships can help us understand the plant economic spectrum, which predicts that leaf and fine root traits are coordinated with carbon allocation (Valverde-Barrantes et al., 2017), therefore below-ground traits constitute a knowledge gap in the plant economic spectrum in tropical forests with different environmental gradients.

5.4.4 Conclusions

The dataset spans an elevation gradient of over 3500 m, from dry lowland Amazon forests to tree line montane forests of the Andes. To our best knowledge, this is the first study in tropical forests that reports seasonal variation reports of monthly fine root productivity and mortality by soil depth. This unique dataset allows us to explore the factors driving the variation in fine root dynamics (productivity, mortality and residence time) with soil depth; and to compare the

seasonal variation in fine root productivity and mortality against precipitation patterns across Amazon and Andes forests.

The intensive measurements and long-term dataset of this study provide a new understanding of fine root dynamics across Andean montane and Amazon lowland forests. We found that fine root carbon stock decreased with soil depth, and soil organic thickness was positively related to root carbon stock. Annual root productivity and mortality decreased with soil depth and the highest root productivity was recorded in the organic layer, the thickness of which increased with elevation. The seasonal variation of root productivity and mortality was driven by precipitation, mortality exceeding productivity in the driest and wettest months. In addition, our results highlight the advantages of rhizotron technique that revealed for the first time that root mortality increased in dry and wet montane forests.

The rhizotron technique used in this study helped us understand fine root productivity and mortality at different soil depths with high accuracy in lowland and montane forests. Ingrowth core technique may have less accuracy in montane forests which may be related to the thick soil organic layer. This assembled the largest dataset of fine root dynamics and comprehensively demonstrates the drivers of fine root dynamics across an elevational gradient, which is also a temperature gradient, and across neotropical forest types. Our results suggest that differences in soil water availability, soil nutrient content, and forest structure in Andean and Amazon forests play a key on fine root dynamics and their response to changes in climate.

5.5 Acknowledgements

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5.6 References

Addo-Danso, S. D., Prescott, C. E., & Smith, A. R. (2016). Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. *Forest Ecology and Management*, *359*, 332–351. https://doi.org/10.1016/j.foreco.2015.08.015

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Araujo-Murakami, A., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Arroyo, L., Heredia, J. P., … Malhi, Y. (2014). The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecology & Diversity*, *7*(1–2), 55–69. https://doi.org/10.1080/17550874.2013.798364

Assefa, D., Rewald, B., Sandén, H., & Godbold, D. L. (2017). Fine Root Dynamics in Afromontane Forest and Adjacent Land Uses in the Northwest Ethiopian Highlands. *Forests*, *8*(7), 249. https://doi.org/10.3390/f8070249

Bahar, N. H. A., Ishida, F. Y., Weerasinghe, L. K., Guerrieri, R., O'Sullivan, O. S., Bloomfield, K. J., … Atkin, O. K. (2017). Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation Andean tropical moist forests of Peru. *New Phytologist*, *214*(3), 1002–1018. https://doi.org/10.1111/nph.14079

Bernier, P. Y., & Robitaille, G. (2004). A plane intersect method for estimating fine root productivity of trees from minirhizotron images. *Plant and Soil*, *265*(1–2), 165–173. https://doi.org/10.1007/s11104-005-0056-y

Bilic-Zulle, L. (2011). Comparison of methods: Passing and Bablok regression. *Biochemia Medica*, *21*(1), 49–52. https://hrcak.srce.hr/64499

Blonder, B., Salinas, N., Bentley, L. P., Shenkin, A., Chambi Porroa, P. O., Valdez Tejeira, Y., … Malhi, Y. (2018). Structural and defensive roles of angiosperm leaf venation network reticulation across an Andes-Amazon elevation gradient. *Journal of Ecology*, *106*(4), 1683–1699. https://doi.org/10.1111/1365-2745.12945

Campos C., A., Cruz H., L., & Rocha O., S. (2017). Mass, nutrient pool, and mineralization of litter and fine roots in a tropical mountain cloud forest. *Science of The Total Environment*, *575*, 876–886. https://doi.org/10.1016/j.scitotenv.2016.09.126

Cavelier, J., Wright, S. J., & Santamaria, J. (1999). Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. *Plant and Soil*, *211*(2), 207–213. https://doi.org/10.1023/A:1004686204235

Chairungsee, N., Gay, F., Thaler, P., Kasemsap, P., Thanisawanyangkura, S., Chantuma, A., & Jourdan, C. (2013). Impact of tapping and soil water status on fine root dynamics in a rubber tree plantation in Thailand. *Frontiers in Plant Science*, *4*, 538. https://doi.org/10.3389/fpls.2013.00538

Chen, X., Eamus, D., & Hutley, L. B. (2004). Seasonal patterns of fine-root productivity and turnover in a tropical savanna of northern Australia. *Journal of Tropical Ecology*, *20*(2),

221–224. https://doi.org/10.1017/S0266467403001135

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde-Barrantes, O., Fuchslueger, L., Oblitas, E., … Quesada, C. A. (2020). Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant-Environment Interactions*, *1*(1), 3–16. https://doi.org/10.1002/pei3.10010

da Costa, A. C. L., Metcalfe, D. B., Doughty, C. E., de Oliveira, A. A. R., Neto, G. F. C., da Costa, M. C., … Malhi, Y. (2014). Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest. *Plant Ecology & Diversity*, *7*(1–2), 7–24. https://doi.org/10.1080/17550874.2013.798366

Doughty, C. E., Metcalfe, D. B., da Costa, M. C. L., de Oliveira, A. A. R., Neto, G. F. C., Silva, J. A., … Malhi, Y. (2014). The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil. *Plant Ecology & Diversity*, *7*(1–2), 41–53. https://doi.org/10.1080/17550874.2013.798367

Doughty, C. E., Metcalfe, D. B., Girardin, C. A. J., Amézquita, F. F., Cabrera, D. G., Huaraca Huasco, W., … Malhi, Y. (2015). Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, *519*(7541), 78–82. https://doi.org/10.1038/nature14213

Endo, I., Kume, T., Kho, L. K., Katayama, A., Makita, N., Ikeno, H., … Ohashi, M. (2019). Spatial and temporal patterns of root dynamics in a Bornean tropical rainforest monitored using the root scanner method. *Plant and Soil*, *443*(1–2), 323–335. https://doi.org/10.1007/s11104-019-04203-w

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., … Woodward, F. I. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2 . *Proceedings of the National Academy of Sciences*, *111*(9), 3280–3285. https://doi.org/10.1073/pnas.1222477110

Galbraith, D., Malhi, Y., Affum-Baffoe, K., Castanho, A. D. A., Doughty, C. E., Fisher, R. A., … Lloyd, J. (2013). Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity*, *6*(1), 139–157. https://doi.org/10.1080/17550874.2013.770578

Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082

Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., … Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*(12), 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x

Girardin, Cécile A.J., Espejo, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., … Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

Goldsmith, G. R., Bentley, L. P., Shenkin, A., Salinas, N., Blonder, B., Martin, R. E., … Malhi, Y. (2017). Variation in leaf wettability traits along a tropical montane elevation gradient. *New Phytologist*, *214*(3), 989–1001. https://doi.org/10.1111/nph.14121

Green, J. J., Dawson, L. A., Proctor, J., Duff, E. I., & Elston, D. A. (2005). Fine Root Dynamics in a Tropical Rain Forest is Influenced by Rainfall. *Plant and Soil*, *276*(1–2), 23–32. https://doi.org/10.1007/s11104-004-0331-3

Gvozdevaite, A., Oliveras, I., Domingues, T. F., Peprah, T., Boakye, M., Afriyie, L., … Malhi, Y. (2018). Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–savanna boundaries in Ghana and Brazil. *Tree Physiology*, *38*(12), 1912–1925. https://doi.org/10.1093/treephys/tpy117

Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., & Leuschner, C. (2009). Below- and above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi, Indonesia) as compared to neotropical forests. *Forest Ecology and Management*, *258*(9), 1904–1912. https://doi.org/10.1016/j.foreco.2009.07.019

Huaraca Huasco, W., Riutta, T., Girardin, C. A. J., Hancco Pacha, F., Puma Vilca, B. L., Moore, S., … Malhi, Y. (2021). Fine root dynamics across pantropical rainforest ecosystems. *Global Change Biology*, *27*(15), 3657–3680. https://doi.org/10.1111/gcb.15677

Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042

Ibrahima, A., Mvondo ZE, A., & Ntonga, J. (2010). Fine root production and distribution in the tropical rainforests of south-western Cameroon: effects of soil type and selective logging. *IForest - Biogeosciences and Forestry*, *3*(5), 130–136. https://doi.org/10.3832/ifor0549-003

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., … Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26. https://doi.org/10.1111/nph.14486

Jiménez, E. M., Peñuela-Mora, M. C., Moreno, F., & Sierra, C. A. (2020). Spatial and temporal variation of forest net primary productivity components on contrasting soils in northwestern Amazon. *Ecosphere*, *11*(8). https://doi.org/10.1002/ecs2.3233

Katayama, A., Kho, L. K., Makita, N., Kume, T., Matsumoto, K., & Ohashi, M. (2019). Estimating Fine Root Production from Ingrowth Cores and Decomposed Roots in a Bornean Tropical Rainforest. *Forests*, *10*(1), 36. https://doi.org/10.3390/f10010036

Malhi, Y., del Aguilla-Pasquell, J., Metcalfe, D. B., Phillips, O. L., Farfan-Rios, W., Silman, M., … Farfán Amézquita, F. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Malhi, Y., Farfán Amézquita, F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., … Phillips, O. L. (2014). The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology and Diversity*, *7*(1–2), 85–105. https://doi.org/10.1080/17550874.2013.820805

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E. O. C., Rifai, S. W., … Phillips, O. L. (2021). The Global Ecosystems Monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. *Biological Conservation*, *253*, 108889. https://doi.org/10.1016/j.biocon.2020.108889

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P., & Saatchi, S. (2010). Introduction: Elevation gradients in the tropics: Laboratories for ecosystem ecology and global change research. *Global Change Biology*, *16*(12), 3171–3175. https://doi.org/10.1111/j.1365-2486.2010.02323.x

Manuilova, E., Schuetzenmeister, A., & Model, F. (2015). Package 'mcr.' Retrieved from https://mran.microsoft.com/snapshot/2014-11-17/web/packages/mcr/mcr.pdf

Marthews, T. R., Riutta, T., Menor, I. O., Urrutia, R., Moore, S., Metcalfe, D., … Networks, C. R. and colleagues from the R. and G. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0, 121.

Metcalfe, D. B., Meir, P., & Williams, M. (2007). A comparison of methods for converting rhizotron root length measurements into estimates of root mass production per unit ground area. *Plant and Soil*, *301*(1–2), 279–288. https://doi.org/10.1007/s11104-007-9447-6

Metcalfe, D. B., Phillips, O., Baker, T., & Brienen, R. (2009). Measuring Tropical Forest Carbon Allocation And Cycling. *RAINFOR Field Manual*, (June), 1–24.

Metcalfe, D. B., Williams, M., Aragão, L. E. O. C., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., … Meir, P. (2007). A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. *The New Phytologist*, *174*(3), 697–703. https://doi.org/10.1111/j.1469-8137.2007.02032.x

Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., & Hertel, D. (2010). Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity*, *3*(2), 151–164. https://doi.org/10.1080/17550874.2010.517788

Nakahata, R., & Osawa, A. (2017). Fine root dynamics after soil disturbance evaluated with a root scanner method. *Plant and Soil*, *419*(1–2), 467–487. https://doi.org/10.1007/s11104-017-3361-3

Okada, K., Aiba, S., & Kitayama, K. (2017). Influence of temperature and soil nitrogen and phosphorus availabilities on fine-root productivity in tropical rainforests on Mount Kinabalu, Borneo. *Ecological Research*, *32*(2), 145–156. https://doi.org/10.1007/s11284-016-1425-0

Passing, H., & Bablok, W. (1983). A New Biometrical Procedure for Testing the Equality of Measurements from Two Different Analytical Methods. Application of linear regression procedures for method comparison studies in Clinical Chemistry, Part I. *Clin. Chem. Clin. Biochem.*, *21*(11), 709–720. https://doi.org/10.1515/cclm.1983.21.11.709

Peixoto, K. S., Marimon-Junior, B. H., Marimon, B. S., Elias, F., de Farias, J., Freitag, R., … Malhi, Y. (2017). Unravelling ecosystem functions at the Amazonia-Cerrado transition: II. Carbon stocks and CO 2 soil efflux in cerradão forest undergoing ecological succession. *Acta Oecologica*, *82*, 23–31. https://doi.org/10.1016/j.actao.2017.05.005

Priess, J., Then, C., & Fölster, H. (1999). Litter and fine-root production in three types of tropical premontane rain forest in SE Venezuela. *Plant Ecology*, *143*(2), 171–187. https://doi.org/10.1023/A:1009844226078

Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., … Paiva, R. (2009). Chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences Discussions*, *6*(2), 3923–3992. https://doi.org/10.5194/bgd-6-3923-2009

Quesada, Carlos Alberto, Paz, C., Oblitas Mendoza, E., Phillips, O., Saiz, G., & Lloyd, J. (2020). Variations in soil chemical and physical properties explain basin-wide variations in Amazon forest soil carbon densities. *Soil*, 1–62. https://doi.org/10.5194/soil-6-53-2020

Rapp, J. M., Silman, M. R., Clark, J. S., Girardin, C. A. J., Galiano, D., & Tito, R. (2012). Intra- and interspecific tree growth across a long altitudinal gradient in the Peruvian Andes. *Ecology*, *93*(9), 2061–2072. https://doi.org/10.1890/11-1725.1

Rocha, W., Metcalfe, D. B., Doughty, C. E., Brando, P., Silvério, D., Halladay, K., … Malhi, Y. (2014). Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). *Plant Ecology & Diversity*, *7*(1–2), 25–40. https://doi.org/10.1080/17550874.2013.798368

Röderstein, M., Hertel, D., & Leuschner, C. (2005). Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, *21*(5), 483–492. https://doi.org/10.1017/S026646740500249X

Sierra Cornejo, N., Hertel, D., Becker, J. N., Hemp, A., & Leuschner, C. (2020). Biomass, Morphology, and Dynamics of the Fine Root System Across a 3,000-M Elevation Gradient on Mt. Kilimanjaro. *Frontiers in Plant Science*, *11*, 13. https://doi.org/10.3389/fpls.2020.00013

Soethe, N., Lehmann, J., & Engels, C. (2006). The Vertical Pattern of Rooting and Nutrient

Uptake at Different Altitudes of a South Ecuadorian Montane Forest. *Plant and Soil*, *286*(1–2), 287–299. https://doi.org/10.1007/s11104-006-9044-0

Soethe, Nathalie, Lehmann, J., & Engels, C. (2007). Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. *Journal of Tropical Ecology*, *23*(3), 319–328. https://doi.org/10.1017/S0266467407004002

Telles, E. de C. C., de Camargo, P. B., Martinelli, L. A., Trumbore, S. E., da Costa, E. S., Santos, J., … Oliveira, R. C. (2003). Influence of soil texture on carbon dynamics and storage potential in tropical forest soils of Amazonia. *Global Biogeochemical Cycles*, *17*(2). https://doi.org/10.1029/2002GB001953

Trumbore, S., Da Costa, E. S., Nepstad, D. C., Barbosa De Camargo, P., Martinelli, L. a., Ray, D., … Silver, W. (2006). Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology*, *12*(2), 217–229. https://doi.org/10.1111/j.1365-2486.2005.001063.x

Valverde-Barrantes, O. J., Freschet, G. T., Roumet, C., & Blackwood, C. B. (2017). A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytologist*, *215*(4), 1562–1573. https://doi.org/10.1111/nph.14571

Van Do, T., Sato, T., & Kozan, O. (2016). A new approach for estimating fine root production in forests: a combination of ingrowth core and scanner. *Trees*, *30*(2), 545–554. https://doi.org/10.1007/s00468-015-1195-2

Vogt, K. A., Vogt, D. J., & Bloomfield, J. (1998). Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. *Plant and Soil*, *200*(1), 71–89. https://doi.org/10.1023/A:1004313515294

Wood, S. (2019). *Package 'mgcv.' Version 1.8-29*. https://doi.org/10.1201/9781315370279

Yavitt, J. B., Harms, K. E., Garcia, M. N., Mirabello, M. J., & Wright, S. J. (2011). Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. *Austral Ecology*, *36*(4), 433–445. https://doi.org/10.1111/j.1442-9993.2010.02157.x

Zhu, F., Yoh, M., Gilliam, F. S., Lu, X., & Mo, J. (2013). Nutrient Limitation in Three Lowland Tropical Forests in Southern China Receiving High Nitrogen Deposition: Insights from Fine Root Responses to Nutrient Additions. *PLoS ONE*, *8*(12), e82661. https://doi.org/10.1371

5.7 Supplementary material

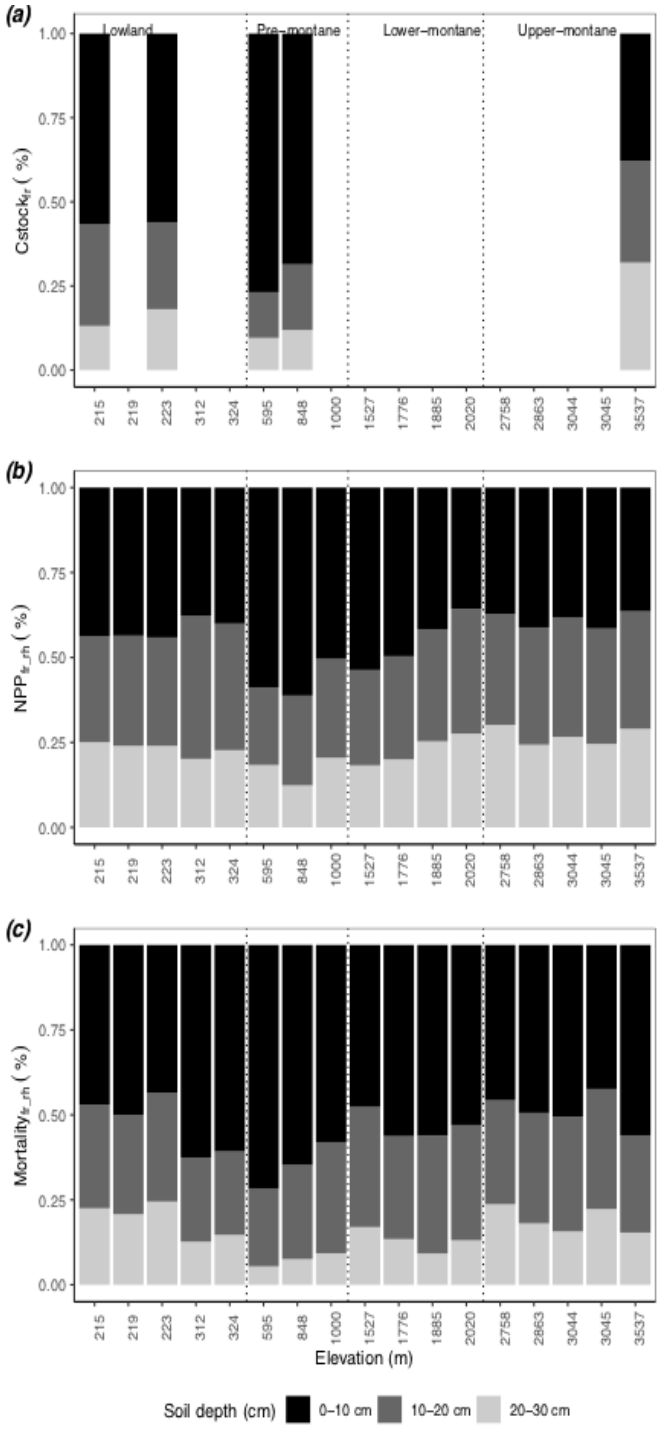


Figure S5.1. (a) Distribution of fine root C stock ($Cstock_{fr}$), (b) productivity (NPP_{fr_rh}), and (c) mortality ($Mortality_{fr}$) recorded with soil core and rhizotron techniques at three soil depths of 0-10 cm, 10-20 cm, and 20-30 cm from lowland to montane forests. Dotted lines separate the forest types of lowland, pre-montane, lower-montane, and upper-montane forests.

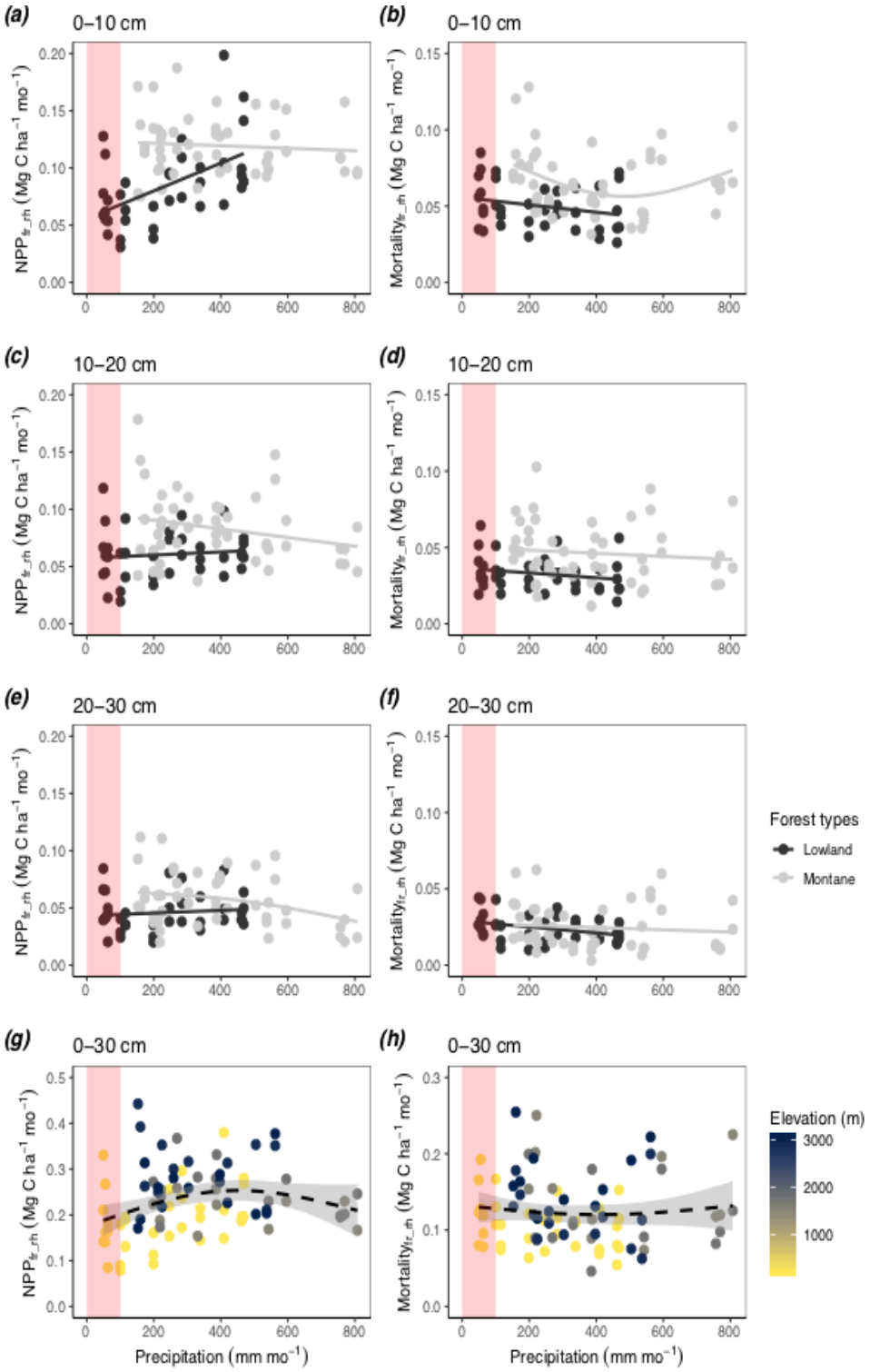


Figure S5.2. Generalised additive model (GAM) predictions of the relationship between elevation and fine root productivity and mortality recorded with rhizotron technique in the 0-10 cm soil depth layer (a, b), 10-20 cm layer (c, d), and 20-30 cm layer (e, f) in lowland and montane forests, and total depth (0-30 cm) (g, h) across elevations. The red vertical shadow areas indicate the monthly precipitation under 100 mm mo^{-1} during dry months. The grey band shows the 95% on panel (g) and (h) of the confidence interval of the model prediction.

Chapter 6: Fine root morphological traits along an elevation gradient in Amazonian-Andean tropical rainforests

In the previous chapter, I reported the vertical profile and seasonal variation of fine root dynamics recorded with ingrowth and rhizotron methods. However, focusing solely on biomass production and carbon dynamics might limit our understanding on root strategies. Therefore, in this chapter, I examine fine root morphological traits (specific root length, specific root area and root tissue density) and fine root morphological dynamics (length growth and surface area growth). To understand the variation from lowland Amazon moist forests to montane Andean forests in southeast Peru, data were collected in fifteen forest sites for several years. I also use the data recorded with the ingrowth core technique in chapter 5 to examine the relationship between root carbon dynamics and root morphological traits. Finally, I analyse the relationships of root morphological traits and dynamics with soil properties, and climatic data.

I conceived this paper together with my supervisors and led on data processing, analysis and writing. I directly collected data from the Peruvian sites, and played a leading role in developing the protocol and training data collectors in the other sites. Other co-authors collected and provided data from the other field sites. This paper was submitted to *New Phytologist* in April 2021.

Title: Fine root morphological traits along an elevation gradient in Amazonian-Andean tropical rainforests

Authors: Walter Huaraca Huasco[1*], Terhi Riutta[1], Cecile A. J. Girardin[1], Beisit L. Puma Vilca[2], Fernando Hancco Pacha[2], Dan Metcalfe[3], Judith M. Laupa Roman[2], Mary L Ortiz de Orue[2], Luis M. Alvarez Mayorga[2], Maria E. Ezquerra Condori[2], Darcy F. Galiano Cabrera[2], Jimmy R. Chambi Paucar[2], Yulin Mamani Gutierrez[2], Rosi Mamani Tacusi[2], Liliana Durand Baca[4], Jose Kala Mamani[2], Oliver Philips[5], Patrick Meir[6], Miles Silman[7], and Yadvinder Malhi[1]

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* Author for correspondence: **Walter Huaraca Huasco (stwamayr@gmail.com)**

[1] (Huaraca Huasco; Riutta; Girardin; Malhi) Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

[2] (Hancco Pacha; Puma Vilca; Laupa Roman; Galiano Cabrera; Ortiz de Orue; Alvarez Mayorga; Ezquerra Condori; Galiano Cabrera; Chambi Paucar; Mamani Gutierrez; Mamani Tacusi) Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú

[3] (Metcalfe) Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

[4] (Durand Baca) Universidad Nacional Federico Villarreal de Lima, Lima, Perú

[5] (Phillips) School of Geography, University of Leeds, UK

[6] (Meir) Research School of Biology, Australian National University, ACT 2602 Australia

[7] (Silman) Department of Biology, Wake Forest University, Winston-Salem, NC 27106, US

Abstract

Fine root morphological traits and dynamics are key features of belowground ecosystem functioning. However, the relationship between root morphological traits and soil properties and climatic variables is poorly understood. We report the variation of fine root morphological dynamics of fine root length growth rate and root surface area growth rate and morphological traits of specific root length (SRL), specific root surface area (SRA), and root tissue density (RTD) by 1 mm diameter classes along a 3000 m tropical forest elevation gradient in the Amazon-Andes region. Production of fine root biomass does not vary with elevation. However, the rate of production of new fine root length and surface area shows a strong mid-elevation peak. This seemingly contradictory finding is driven by root tissue density, which has its lowest values at mid elevations. Variation in root tissue density explains almost all variation in SRL and SRA; variation in root size distribution has negligible influence. No strong relationships were found between root traits and root carbon dynamics (root mass production rates and residence times, fractional allocation of total net primary productivity to the fine roots). Fine root morphological traits and dynamics were strongly driven by soil properties, which explained between 71% and 83% of the variation in the data. Root length and surface area production rates increased with soil sand content and decreased with cation exchange capacity (CEC). SRL and SRA increased with soil C:N ratio and soil phosphorus (P), but decreased with CEC. RTD decreased with increasing P content, but increased with CEC. Our study highlights the importance of variation in root tissue density in determining root morphological traits and the rate of root foraging for resources (root length and surface area production). Considering root biomass production rates alone can miss important variation in rates of resource foraging by roots, and important root-environment relationships.

Key words: Root morphological traits, specific root length, specific surface area, root tissue density

6.1 Introduction

Fine roots perform the key ecosystem function of water and nutrient uptake. Most studies on ecosystem carbon dynamics focus on the stock and production of root biomass. However, for a given biomass, root length, diameter and density distributions may vary across ecosystem types and environmental gradients. Therefore, root morphological traits, rather than biomass alone, may offer better insights into root strategies and root-environment relationships. Nutrient poor and dry ecosystems require more efficient resource foraging by roots than nutrient rich and wet ecosystems. In such ecosystems, plants may invest more in fine root biomass production, or as an alternative or complementary strategy, may produce lighter and/or thinner roots with relatively greater length and surface area per unit mass, as discussed by Metcalfe et al. (2008). On the other hand, nutrient poor soils may favour more conservative traits, such as high root tissue density and longer life span, over rapid root growth (Freschet et al., 2021).

The external shape of roots, root length, root surface area, root diameter, root tissue density, specific root length (SRL), specific root surface area (SRA), and root hair density are the most commonly studied morphological root dynamics and morphological root traits (Freschet et al., 2021; McCormack et al., 2017). These dynamics and traits vary across edaphic and climatic gradients. In particular, soil P limitation has been identified as a key factor for root hair production, root clustering, root lifespan, and fungal community associations (Lambers et al., 2006; McCormack & Guo, 2014).

Root length and surface area growth have been reported to increase with decreasing soil nutrient contents in tropical forests (Freschet et al., 2021). Similarly, a tropical forest fertilisation experiment has shown that the addition of nitrogen, phosphorus, and potassium reduce root productivity and length (Wurzburger & Wright, 2015). Increasing soil carbon to nitrogen ratio increases root length growth (Graefe et al., 2008). As the C:N ratio increases

with increasing elevation in tropical montane forests (Graefe et al., 2008; Moser et al., 2010; Sierra Cornejo et al., 2020), it may drive the elevational patterns in root traits. Soil sand content has a positive relationship with root length and surface area growth (Kochsiek, Tan, & Russo, 2013), plant communities increasing their root absorptive area in sandy tropical soils (Germon et al., 2020; Hendricks et al., 2006; Silver et al., 2005).

The most quantified root morphological traits, SRL and SRA, are defined as the total root length and surface area growth per unit root dry mass, respectively. Tropical forest studies report that soil P is positively related to SRL in natural soil P gradients (Hogan et al., 2020). In a tropical fertilisation experiment, SRL increased in N+P and N+P+K treatments (Wurzburger & Wright, 2015). Furthermore, increasing root branching intensity to uptake soil resources is positively related to SRL (Eissenstat et al., 2015; Kramer-Walter et al., 2016), which may reflect alternative foraging strategies and mycorrhizal associations. Soil P limitation has been identified as a key factor in controlling root hair production, root clustering, root lifespan, and fungal community association (Lambers et al., 2006).

Root tissue density (RTD) is the ratio of dry mass per unit volume and determined by the cortex and stele anatomical and chemical traits (Birouste et al., 2014; Kong et al., 2019). RTD is positively correlated with root residence time and negatively correlated with root respiration (Makita et al., 2012; Reich, 2014). SRA is negatively related to RTD as an ecological strategy (Addo-Danso et al., 2018), high SRA being an acquisitive trait and high RTD a conservative trait. Therefore, fast growing tree species typically have high SRL and SRA but low RTD (Assefa et al., 2018). Furthermore, low RTD is usually related to high aboveground biomass and basal area (Sierra Cornejo et al., 2020). Of the different belowground traits, RTD has the most consistent, negative response to soil fertility (Kramer-Walter et al., 2016; Wang et al., 2018). In a tropical forest fertilization experiment, the RTD declined in response to K, N+P, and K+N+P treatments (Wurzburger & Wright, 2015).

Compared to soil variables, the effect of climatic variables on root morphological traits has been less explored. A review on the tropical forest root morphological traits reported that changes in mean annual precipitation and temperature had no significant influence on root morphological traits, except for temperature explaining a small proportion of the variation in SRL (Addo-Danso et al., 2020). Precipitation was positively related to root diameter and SRA in an elevational transect in Mount Kilimanjaro (Sierra Cornejo et al., 2020). Root morphological traits may also have seasonal dynamics related to climatic variables: root length and surface area growth increased with increasing precipitation during the rainy season in tropical lowland forests (Andrade et al., 2020; Metcalfe et al., 2008).

Fine roots comprise functionally different absorptive roots (1st and 2nd order roots) and transport roots (3rd and higher order roots). To improve our understanding of root morphological traits, an analysis across size classes may reveal how different plant species have developed their strategies to increase water and nutrient acquisition (McCormack & Iversen, 2019). In their review of fine root morphological traits in tropical forests, Addo-Danso et al. (2020) also highlight the need to examine fine root traits-environment relationships by root functional types and size classes as a key research need. Such an approach may also help us better understand the associations with mycorrhizal fungi and adaptations to soil environment (Kong et al., 2017).

We quantify fine root morphological traits in old-growth forest ecosystems from lowland Amazon to Andean forests on an elevation gradient that ranges from 215 m asl to 3500 m asl. Morphological dynamics of root length growth and surface area growth, and morphological traits of specific root length, specific root surface area, and root tissue density were recorded by intensive measurements. This study addressed the following three questions: (1) How do fine root morphological dynamics and morphological traits vary from lowland to montane forests?

(2) Are changes in root morphological dynamics and traits driven by changes in root size distribution or by root tissue density or some combination of both?

(3) How are fine root morphological traits related to root dynamics and soil characteristics?

6.2 Materials and methods

6.2.1 Study area

Fine root morphological traits study was carried out in two protected areas of Tambopata National Reserve and Manu National Park in Peru. These protected areas are located in Madre de Dios and Cusco regions, respectively, that cover the Amazon and Andes regions of Peruvian rainforest ecosystems. This study was part of large projects carried out by The Global Ecosystem Monitoring Network (GEM) and The Amazon Forest Inventory Network (RAINFOR) since 2006 until 2017, where we conducted intensive monitoring of fine root carbon allocation across fifteen one-hectare permanent plots from lowland wet forests to upper montane forests. Three lowland wet forest plots are located in Tambopata Reserve (TAM-05, TAM-06, TAM-09) and are situated on infertile Cambisol soil (TAM-05) and fertile Haplic Alisol soil (TAM-06) (Aragão et al., 2009; Rowland et al., 2014). The montane sites comprised three plots in pre-montane forests (PAN-02, PAN-03, TON-01), four plots in lower montane forests (SPD-02, SPD-01, TRU-08, TRU-07), and five plots in upper montane forests (TRU-04, TRU-03, ESP-01, WAY-01, ACJ-01) (Table 6.1). The mean annual temperature, precipitation, and other climatic and soil variables of our study plots are listed on Table 6.1. The seasonal pattern is similar across the elevation gradient, with the highest precipitation between November and January and lowest precipitation between April and August, but the monthly and annual rates vary (Girardin et al., 2010; Girardin et al., 2014; Huaraca Huasco et al., 2014; Malhi et al., 2017). The data collection period for each plot is shown in Table 6.2, ranging from nine months to four years.

6.2.2 Fine root morphological traits sampling and sample processing

We used the ingrowth core method for estimating fine root productivity (NPP_{fr}) and for collecting root samples for morphological trait quantification. Cylindrical ingrowth cores with a size of 12 cm diameter and 40 cm length made of plastic wire mesh were used to record fine root morphological and dynamic traits. We installed nine cores in TON-1, TRU-08, TRU-07 and TRU-03 plots, and 16 cores in the other plots. During the ingrowth core installation, fine root carbon stock ($Cstock_{fr}$) was recorded collecting soil core samples with a diameter of 12 cm and total soil depth of 30 cm. Soil cores were separated into organic and mineral layers, the thickness of which were measured, and all roots were collected manually from each soil layer, following the GEM protocol (Marthews et al., 2014; Metcalfe et al., 2007). The wire mesh ingrowth core was placed into the hole, which was back-filled with this newly root-free soil, following the order of soil layers to avoid soil translocation from top to bottom. The ingrowth cores were harvested every three months, following the same protocol that was used to record root carbon stock during the ingrowth cores installation. Fine roots were extracted manually for a period of forty minutes (4 × 10 min). This technique keeps the search time in the field reasonable, while enabling us to estimate the proportion of the roots that remained in the sample. Root samples were cleaned by rinsing in water, using fine sieves, to remove the organic and mineral soil particles. Rinsed roots were scanned on Canon LiDE 220 flatbed scanner. WinRhizo Pro version 2019 (Regent Instruments inc., Canada) was used to analyse the scanned images and then to calculate the total root length (LEN_{fr}, km m^{-2} yr^{-1}), surface area (SA_{fr}, m^2 m^{-2} yr^{-1}), and volume (VOL_{fr}, cm^3 m^{-2} yr^{-1}) growth during the three-month collection interval by 0.1 mm root diameter classes (Metcalfe et al., 2008). In addition, specific root length (SRL, km kg^{-1}) and specific root surface area (SRA, m^2 kg^{-1}) were calculated by dividing the LEN_{fr} and SA_{fr} by fine root dry biomass, and root tissue density was (RTD, mg cm^{-3}) was estimated by dividing fine root dry biomass by VOL_{fr} (Hogan et al., 2020).

Scanned fine roots samples were oven dried at 70 ^{o}C until constant mass to assess fine root productivity (NPP_{fr}). An asymptotic curve was fitted to the cumulative mass over search time observations and used for predicting the root mass at 120 minutes, as described in previous fine root dynamics studies (Girardin et al., 2013; Metcalfe et al., 2008). We assumed a fine root carbon content of 45% (FRED; roots.ornl.gov; Iversen et al., 2017; Huaraca Huasco et al., 2021). Fractional allocation ($Allocation_{fr}$) of total net primary productivity (NPP_{total}) to fine roots was calculated as NPP_{fr} divided by NPP_{total}, which is the sum of canopy (litterfall and brunch turnover), woody (stem ≥ 10 cm diameter at breast height), fine root (≤ 2 mm) and coarse root (> 2 mm) productivity. NPP_{total} was measured and reported in previous studies across our Andean transect (Girardin et al., 2014, 2010; Huaraca Huasco et al., 2014; Malhi et al., 2017). Fine root residence time (RT_{fr}) was calculated by dividing $Cstock_{fr}$ by the annual average NPP_{fr}.

6.2.3 Soil properties and climatic variables

We collected soil data from all plots, following the consistent RAINFOR protocol (Quesada et al., 2009) and all samples were analysed to a common and cross-calibrated protocol at the INPA soil laboratory in Manaus, Brazil. Mean annual precipitation (MAP) and temperature (MAT) were calculated using data from automatic weather stations installed close to each plot (Table 6.1).

Table 6.1. Characteristics of 1ha permanent plots in lowland, pre-montane, lower montane, and upper montane tropical forest: elevation (Elev, m asl), latitude (Lat., decimal degrees), longitude (Long., decimal degrees), mean annual precipitation (MAP, mm yr^{-1}), mean annual temperature (MAT, ^{o}C), solar radiation (SR, Gj m^{-2} yr^{-1}), and soil properties of soil sand, clay, and silt percentage content (%), total nitrogen (N, %), total carbon-nitrogen ratio (C:N), total phosphorus (P, mg kg^{-1}), total potassium (K, mg kg^{-1}), calcium (Ca, mg kg^{-1}), and soil cation exchange capacity (CEC, mmol+kg^{-1}).

Forest type	Plot code	Elev	Lat.	Long.	MAP	MAT	SR	Sand	Silt	Clay	N	C:N	P	K	Ca	CEC
	TAM-06	215	-12.84	-69.30	2545	24.40	4.80	2.00	52.00	46.00	0.17	7.10	528.80	58.50	536.00	56.80
Lowland	TAM-09	219	-12.83	-69.28	2545	24.40	4.80	NA	NA	NA	NA	NA	NA	NA	NA	NA
(LWF)	TAM-05	223	-12.83	-69.27	2545	24.40	4.80	40.00	17.00	44.00	0.16	9.40	256.30	35.10	6.00	44.80
	PAN-02	595	-12.65	-71.26	2366	23.50	3.82	17.65	37.95	44.40	0.34	10.60	709.00	0.56	NA	NA
Pre-montane	PAN-03	848	-12.64	-71.27	2835	21.90	3.82	44.95	22.65	32.40	0.22	11.30	1174.80	0.42	NA	NA
(PMF)	TON-01	1000	-12.96	-71.57	3087	20.70	NA	27.83	32.42	39.75	0.42	12.22	751.00	154.26	79.20	23.96
	SPD-02	1527	-13.05	-71.54	5302	18.80	4.08	37.51	17.79	44.71	0.88	14.93	1630.71	154.36	183.21	42.21
	SPD-01	1776	-13.05	-71.54	5302	17.40	4.36	31.35	26.97	41.68	1.19	18.01	1071.14	41.79	74.35	32.32
Lower-montane	TRU-08	1885	-13.07	-71.56	2472	18.00	3.96	70.01	20.99	9.00	1.23	21.17	562.83	95.90	75.42	45.47
(LMF)	TRU-07	2020	-13.07	-71.56	1827	17.40	3.96	57.21	26.29	16.50	0.81	17.79	495.97	64.10	78.91	39.84
	TRU-04	2758	-13.11	-71.59	2318	13.50	3.32	13.61	12.50	73.89	1.99	15.47	746.76	182.31	70.93	37.75
	ESP-01	2863	-13.18	-71.59	1560	13.10	4.16	1.37	40.00	58.63	1.48	18.82	980.82	238.10	62.38	35.25
	TRU-03	3044	-13.11	-71.60	1776	11.80	3.49	0.00	0.00	0.00	1.55	16.76	787.31	246.41	68.93	36.07
Upper-montane	WAY-01	3045	-13.19	-71.59	1560	11.80	3.51	43.65	16.50	39.85	0.88	21.23	1413.59	222.26	66.57	42.54
(UMF)	ACJ-01	3537	-13.15	-71.63	1980	9.00	4.23	4.13	56.77	39.10	0.94	12.83	586.93	NA	NA	NA

6.2.4 Statistical analyses

This study focused on the spatial variation of root morphological dynamics and traits (RTD, LEN_{fr}, SA_{fr}, SRL, and SRA) from lowland to upper montane forests. The quarterly estimates from each ingrowth core were averaged to get an annual value for the core. The mean annual estimate and its standard error for each plot was the average annual value of the ingrowth cores within the plot and their standard error of the mean.

We used a generalised additive model (GAM) to examine the relationship between elevation and morphological dynamics and traits of LEN_{fr}, $SA_{fr,}$ RTD, SRL, and SRA of all fine roots ≤ 2 mm diameter, and also by diameter classes of 0.1-0.5 mm, 0.6-1.0 mm, 1.1-1.5 mm, and 1.6-2.0 mm (*mgcv* packages for R, Wood, 2019). The relationships between different morphological traits themselves (SRL vs RTD and SRA vs RTD), and between morphological traits (*S*RL, SRA, and RTD) and fine root dynamics (NPP_{fr}, $Allocation_{fr}$, and RT_{fr}) were analysed using simple linear regression models.

In addition, we examined how soil properties control root morphological dynamics and traits. First, to reduce dimensionality and to identify the most orthogonal soil properties we carried out a principal component analysis (PCA) of soil variables: soil texture (sand, silt, and clay), nitrogen (N), carbon-nitrogen ratio (C:N), phosphorus (P), potassium (K), calcium (Ca), Magnesium (Mg) and soil cation exchange capacity (CEC) (Table S6.1, Figure S6.1), using the factoextra package for R (Kassambara & Mundt, 2020). The variables with the highest loadings on the first four PCA axes, in our case soil sand content, C:N ratio, P content, and CEC, were selected as potential explanatory variables in the models. We used GAM to predict the relationship between explanatory variables and root variables to understand which combination of explanatory variables best explained each root morphological dynamic and trait (length, surface area, specific root length, specific root surface area, and root tissue density). All root morphological variables were modelled using Gamma distribution (values are

positive) with a log link function. Akaike's information criterion (AICc) for small samples was used to compare models and the minimum AIC was selected as the best estimator, using the *MuMln* (Bartón, 2020) package.

To understand how root dynamics and traits (NPP_{fr}, LEN_{fr}, SA_{fr}, SRL, and SRA) by individual 0.1 mm diameter classes relate to soil properties (sand, silt, clay, C:N ratio, P, N, K, Ca, and CEC) and climate variables (MAT, MAP, SR), we calculated the Pearson correlation coefficient (*Hmisc* packages for R, Harrell, 2020) for each pair of abiotic and root variables by diameter class, each plot forming one observation. After obtaining the correlation coefficients for each diameter class, we fitted a GAM model with the correlation coefficient as the response variable and root diameter class as the explanatory variable to describe how the strength and direction of the relationship between root variables and abiotic variables change depending on root size. All statistical analyses were conducted with R statistical software, version 3.6.0.

6.3 Results

6.3.1 Fine root morphological dynamics and traits across the elevation gradient

Fine root productivity did not vary and root residence time increased with elevation (Figure 6.1a, b). Four root morphological variables of LEN_{fr}, SA_{fr}, SRL, and SRA peaked at mid-elevation (Figure 6.1c, d, e, f), while RTD showed the opposite pattern and was at its lowest at mid-elevation (Figure 6.1g). The highest LEN_{fr} and SA_{fr} growth were recorded at 1885 m, and the highest SRL and SRA were recorded at 1527 m (Table 6.2). Increasing elevation increased LEN_{fr} and SA_{fr} growth in the soil organic layer (Figure 6.1c, d), driven by the increase in the soil organic layer thickness.

SRL and SRA across all 0.5 mm root diameter classes peaked at mid-elevation forests (Figure 6.2, Figure S6.2). On the other hand, the proportional contribution of the ≤ 0.5 mm diameter class to total LEN_{fr} and SA_{fr} increased with increasing elevation, while the contribution of the other diameter classes (0.6 mm to 2 mm) decreased with increasing

elevation (Figure 6.2b, Figure S6.2b). Across elevations, the smallest roots had the highest contribution to total fine root length growth, the smallest 0.1-0.5 mm class accounting for approximately 50% of the root length growth (Figure S6.3). For root surface area growth, the contribution of the two smallest diameter classes (0.1-0.5 mm and 0.5-1.0 mm) to total surface area growth was roughly equal, in total approximately 70% (Figure S6.3). In addition, we recorded a tight negative relationship between RTD and SRL and between RTD and SRA (Figure 6.3).

6.3.2 The effect of fine root dynamics and soil properties on fine root morphological traits

Simple linear regressions revealed that fine root dynamics, i.e. fine root productivity, fractional allocation of total NPP to fine roots, and fine root residence time, were not significantly related to fine root morphological traits, i.e. SRL, SRA, and RTD, with the exception of the positive relationship between residence time and SRL (Figure 6.4c, Figure S6.4). On the other hand, GAM models showed that root morphological traits were driven by soil variables: sand content, C:N ratio, P content, and CEC (Table 6.3). LEN_{fr} and SA_{fr} were predicted by sand content and CEC (Figure 6.5a, b), SRL and SRA were predicted by C:N ratio, P, and CEC (Figure 6.5c, d, e), and RTD was predicted by P and CEC (Figure 6.5f, e). These soil variables explained between 71% and 86% of the variation in root morphological traits across the elevation gradient (Table 6.3).

6.3.3 Effect of soil properties and climatic variables on fine root dynamics and traits by 0.1 mm diameter classes.

Fine root morphological dynamics and traits were positively and negatively correlated with soil properties and climatic variables across different root diameter classes (Figure 6.6, Figure S6.5). NPP_{fr} was positively correlated with soil sand content and negatively correlated with soil clay content, but only in the smaller diameter classes, not in the larger ones (Figure 6.6).

LEN_{fr} and SA_{fr} growth were positively correlated with soil sand content, soil C:N ratio, and mean annual precipitation, but negatively correlated with soil clay content (small diameters) and with CEC (large diameters) (Figure 6.6, Figure S6.4). SRL and SRA were negatively correlated with soil silt content and SR and these relationships became stronger with increasing root diameter. They were also positively correlated with soil P and soil C:N ratio, and the relationships became weaker with increasing root diameter (Figure 6.6, Figure S6.4).

Table 6.2. Fine root (≤ 2 mm) dynamics and traits: total length growth (LEN_{fr}, km m^{-2} yr^{-1}), surface area growth (SA_{fr}, m^2 m^{-2} yr^{-1}), specific fine root length (SRL, km kg^{-1}), specific fine root surface area (SRA, m^2 kg^{-1}), root tissue density (RTD, mg cm^{-3}), carbon stock ($Cstock_{fr}$, Mg C ha^{-1}), productivity (NPP_{fr}, Mg C ha^{-1} yr^{-1}), fractional allocation of total net primary productivity to fine roots ($Allocation_{fr}$), and residence time (RT_{fr}, yr). Values are mean and standard error.

Plot code	Elev (m)	Sampling period and Number of replicates	LEN_{fr} mean ± se		SR_{fr} mean ± se		SRL mean ± se		SRA mean ± se		RTD mean ± se		$Cstock_{fr}$ mean ± se		NPP_{fr} mean ± se		$Allocation_{fr}$ mean ± se		RT_{fr} mean ± se	
TAM-06	215	4 years (n=16)	2.24	0.13	4.81	0.28	9.11	1.89	19.55	4.08	218.14	45.61	1.50	0.10	1.11	0.04	0.10	0.01	1.36	0.10
TAM-09	219	9 months (n=16)	4.45	0.58	10.20	1.27	8.90	2.13	20.40	4.81	207.41	48.37	1.78	0.15	2.25	0.38	NA	NA	0.79	0.15
TAM-05	223	4 years (n=16)	5.78	0.30	12.00	0.61	13.76	2.85	28.57	5.90	156.98	32.36	2.36	0.14	1.89	0.07	0.13	0.01	1.25	0.09
PAN-02	595	1 year (n=16)	5.85	0.61	12.70	1.28	13.93	2.21	30.24	4.72	144.60	22.44	2.10	0.18	1.89	0.21	0.20	0.03	1.11	0.16
PAN-03	848	1 year (n=16)	4.14	0.42	8.76	0.88	18.82	3.19	39.82	6.74	110.30	18.56	4.20	0.41	0.99	0.13	0.13	0.02	4.25	0.68
TON-01	1000	1 year (n=9)	7.74	1.02	19.10	2.91	16.13	5.78	39.79	14.58	98.63	36.70	2.37	0.29	2.18	0.73	0.22	0.08	1.09	0.39
SPD-02	1527	9 months (n=16)	7.25	0.93	15.30	1.96	25.89	3.80	54.64	8.01	80.00	11.66	3.12	0.34	1.26	0.09	0.10	0.01	2.48	0.33
SPD-01	1776	9 months (n=16)	8.05	0.79	16.20	1.50	24.39	2.82	49.09	5.43	89.99	9.64	3.73	0.30	1.49	0.07	0.19	0.01	2.51	0.23
TRU-08	1885	1 year (n=9)	13.70	1.56	25.90	3.08	21.08	2.73	39.85	5.34	119.45	16.74	5.95	0.59	2.93	0.16	0.37	0.04	2.03	0.23
TRU-07	2020	1 year (n=9)	8.20	1.25	15.60	2.31	22.78	4.30	43.33	8.02	109.31	20.50	6.25	0.94	1.62	0.16	0.35	0.04	3.85	0.70
TRU-04	2758	1 year (n=16)	4.25	0.43	8.38	0.74	17.71	2.85	34.92	5.34	127.43	19.58	6.20	0.81	1.08	0.14	0.14	0.02	5.74	1.04
ESP-01	2863	9 months (n=16)	6.49	0.94	12.20	1.82	24.96	3.76	46.92	7.23	103.04	15.71	4.85	0.37	1.16	0.05	0.15	0.03	4.18	0.36
TRU-03	3044	1 year (n=9)	6.22	1.21	12.20	1.97	23.92	6.54	46.92	11.78	95.24	23.10	4.53	0.57	1.18	0.21	0.21	0.01	3.84	0.83
WAY-01	3045	2 years (n=2)	5.86	0.64	12.50	1.45	22.54	2.62	48.08	5.88	90.81	11.22	4.68	0.67	1.17	0.06	0.15	0.01	4.00	0.61
ACJ-01	3537	1 year (n=16)	2.22	0.27	4.64	0.61	10.09	3.01	21.09	6.38	206.30	64.25	2.81	0.30	0.97	0.27	0.12	0.03	2.89	0.86

Table 6.3. Summary of generalised additive model (GAM) predictions for fine root length growth (LEN_{fr}, km m^{-2} yr^{-1}), fine root surface area growth (SA_{fr}, m^2 m^{-2} yr^{-1}), specific fine root length (SRL, km kg^{-1}), specific fine root surface area (SRA, m^2 kg^{-1}), and fine root tissue density (RTD, mg cm^3) with soil properties of soil sand content (Sand, %), C:N ratio, P content (mg kg^{-1}), and cation exchange capacity (CEC, mmol+kg^{-1}) as explanatory variables. Estimate for each coefficient, standard error (SE), deviance explained (DE), root mean square error (RMSE), significance of the model coefficients P values (0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1), and Akaike information criterion (AIC) are shown. The best model (lowest AIC) for each response variable is presented here. The full model for each response variable had soil sand content, CEC, C:N ratio and P content as explanatory variables.

Response variables	Explanatory variables	Estimate	SE	*P*	*DE*	*RMSE*	*AIC*
LEN_{fr}	Intercept	2.587569	0.411233	***	71.40%	1.69	53.16
	Sand	0.014081	0.003598	**			
	CEC	-0.028515	0.010012	*			
SR_{fr}	Intercept	3.378132	0.335666	***	79.10%	2.80	64.78
	Sand	0.013935	0.002937	**			
	CEC	-0.030494	0.008172	**			
SRL	Intercept	2.4655237	0.3538953	***	80.50%	2.64	83.81
	CN ratio	0.0454998	0.012442	**			
	P	0.000213	0.0001348				
	CEC	-0.0097236	0.006236				
SRA	Intercept	3.4820946	0.2798045	***	86.10%	4.06	83.25
	CN ratio	0.031557	0.0098372	*			
	P	0.000286	0.0001066	*			
	CEC	-0.0134176	0.0049305	*			
RTD	Intercept	4.3093072	0.2576443	***	82.90%	17.22	103.46
	P	-0.0004389	0.0001123	**			
	CEC	0.0198448	0.0054824	**			

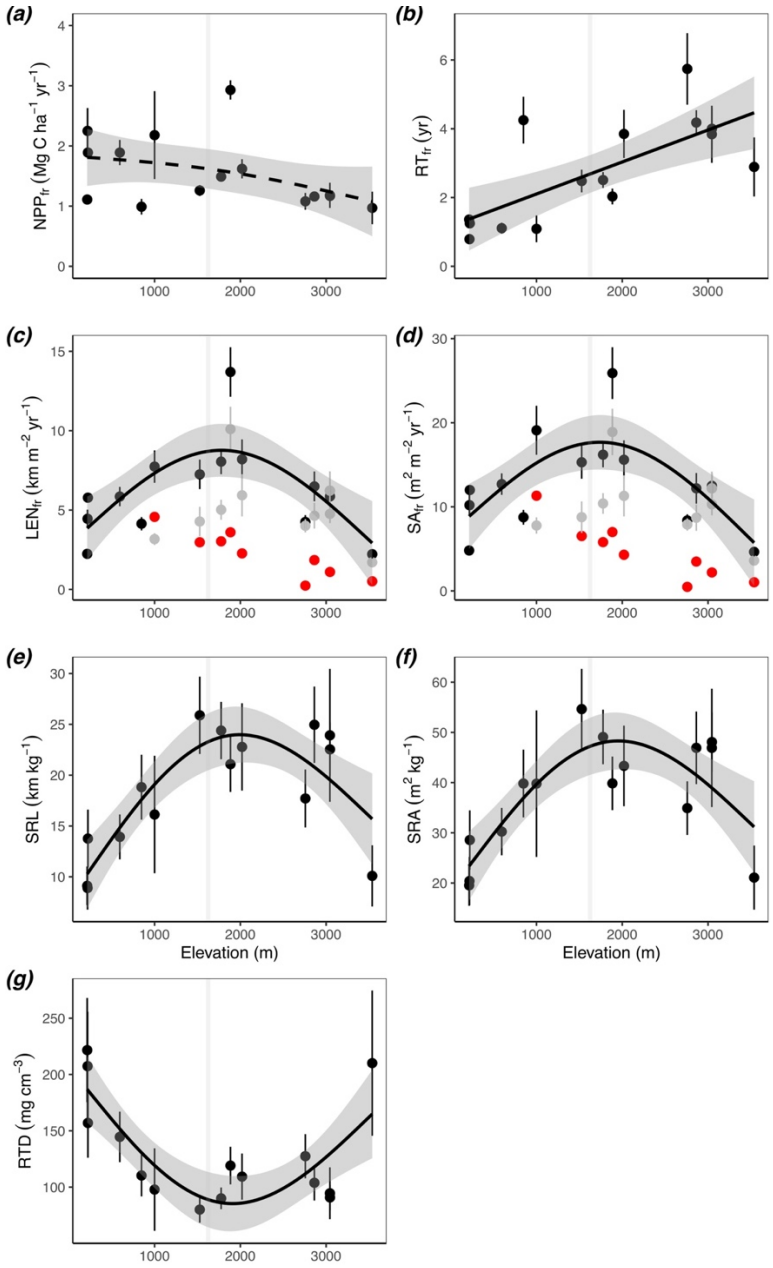


Figure 6.1. The relationship between elevation and (a) fine root productivity (NPP_{fr}, r^2 = 0.13, p = 0.142), (b) fine root residence time (RT_{fr}, r^2 = 0.48, p = 0.00239), (c) fine root length growth (LEN_{fr}, r^2 = 0.50, p = 0.02), (d) fine root surface area growth (SR_{fr}, r^2 = 0.49, p = 0.02), (e) specific fine root length (SRL_{fr}, r^2 = 0.73, p = 0.0007), (f) specific fine root area (SRA_{fr}, r^2 = 0.70, p = 0.002), and (g) fine root tissue density (RTD, r^2 = 0.80, p = 0.0004). Continuous (significant) and dashed (non-significant) lines indicate the generalised additive model predictions and grey bands show the 95% confidence interval for the predictions. The vertical grey line shows the cloud base zone at 1600 m, located in lower montane forests. Grey dots are LEN_{fr} and SA_{fr} growth recorded in the organic layer, red dots are LEN_{fr} and SA_{fr} growth recorded in the mineral layer down to 30 cm depth and black dots are the average of fine root traits across soil layers down to 30 cm depth. Error bars are standard errors of the mean.

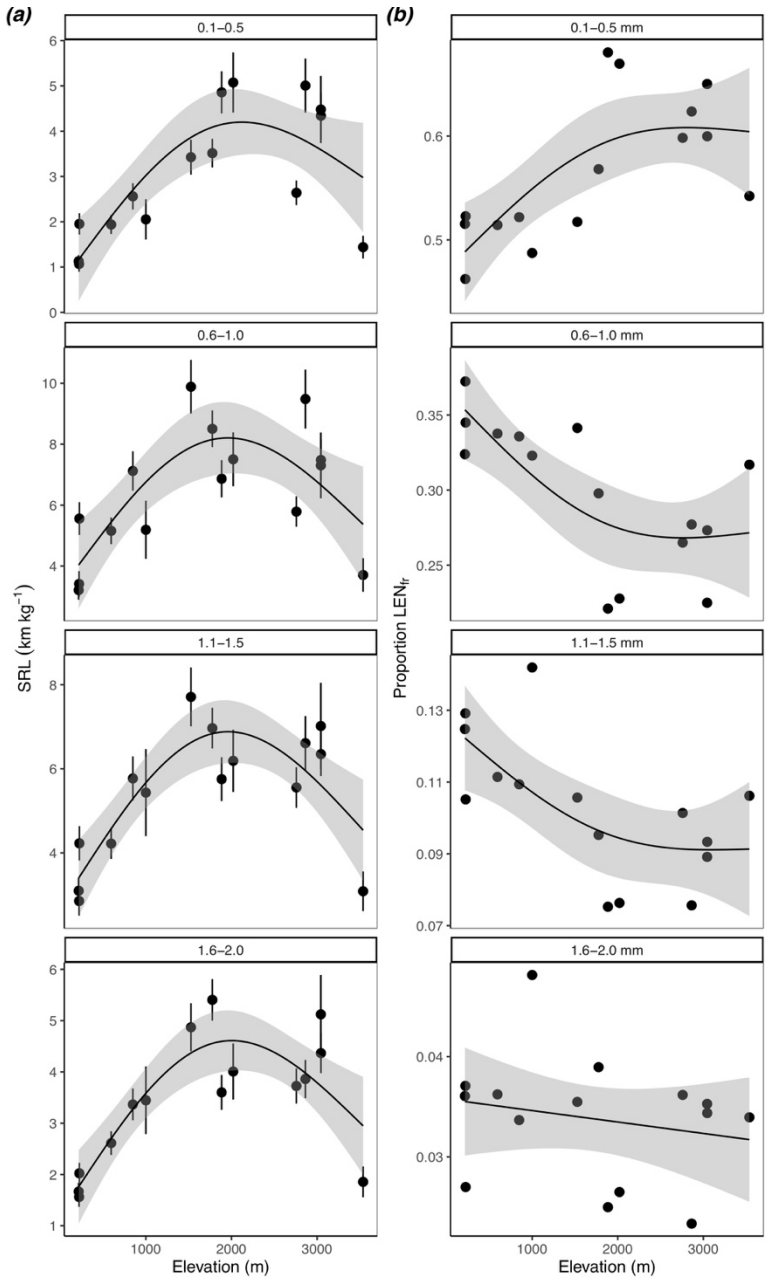


Figure 6.2. The relationship between elevation and (a) specific fine root length (SRL, km kg^{-1}) by root diameter classes, (b) the proportional contribution of each diameter class to total fine root length growth (LEN_{fr}). Continuous black lines are generalised additive model predictions and grey bands show the 95% confidence intervals for the predictions. Error bars are standard errors of the mean.

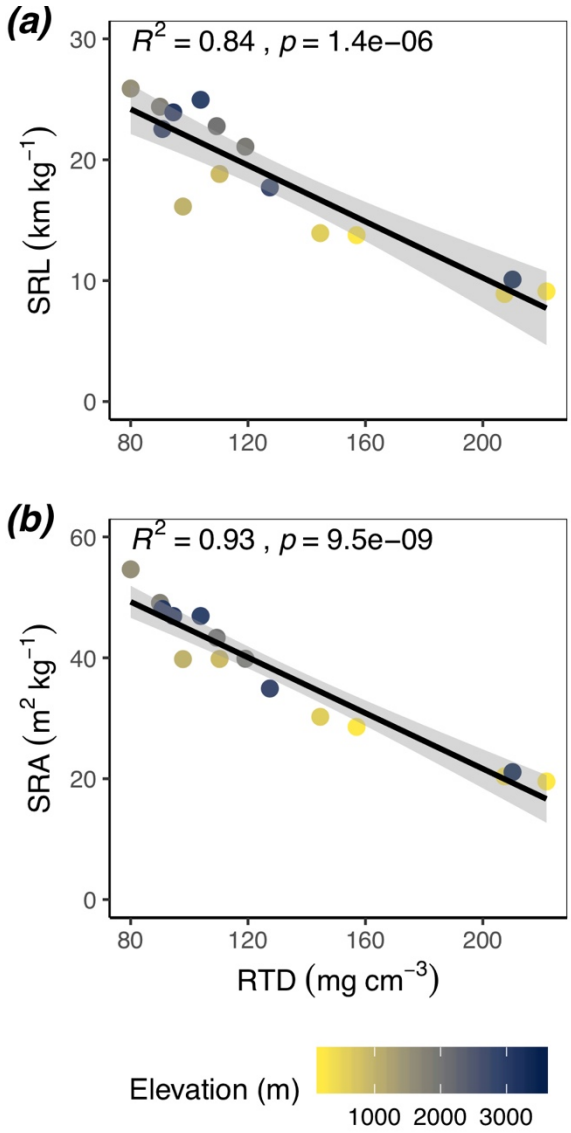


Figure 6.3. The relationship between (a) specific fine root length (SRL, km kg^{-1}) and fine root tissue density (RTD, mg cm^{-3}) (y = a + bx, where a = 263.43 ± 16.62 and b = -7.25 ± 0.86), and (b) specific fine root surface area (SRA, m^2 kg^{-1}) and fine root tissue density (RTD, mg cm^{-3}) (y = a + bx, where a = 282.04 ± 12.28 and b = -4.02 ± 0.31). Continuous black lines show the linear regression line and grey bands show the 95% confidence interval for the predictions. Each data point is a forest plot, coloured by elevation.

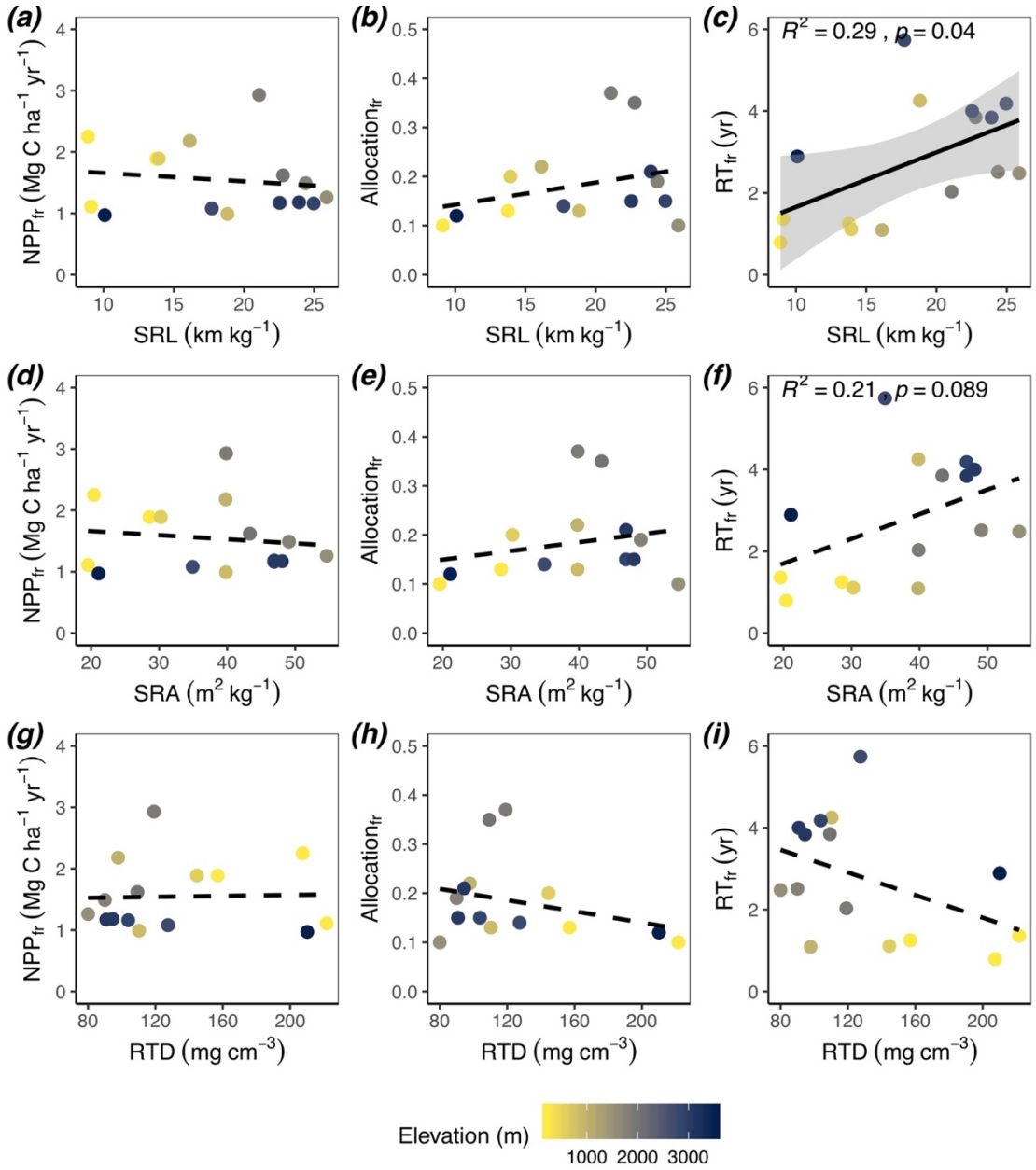


Figure 6.4. The relationship of fine root productivity (NPP_{fr}), fractional allocation of total net primary productivity to fine roots ($Allocation_{fr}$), and root residence time (RT_{fr}) with fine root morphological traits of (a, b, c) specific root length (SRL), (d, e, f) specific root surface area (SRA), and (g, h, i) root tissue density (RTD). The lines are simple linear regressions (continuous line - significant; dotted line - not significant) and the grey band is the 95% confidence interval of the prediction. Each data point is a forest plot, coloured by elevation.

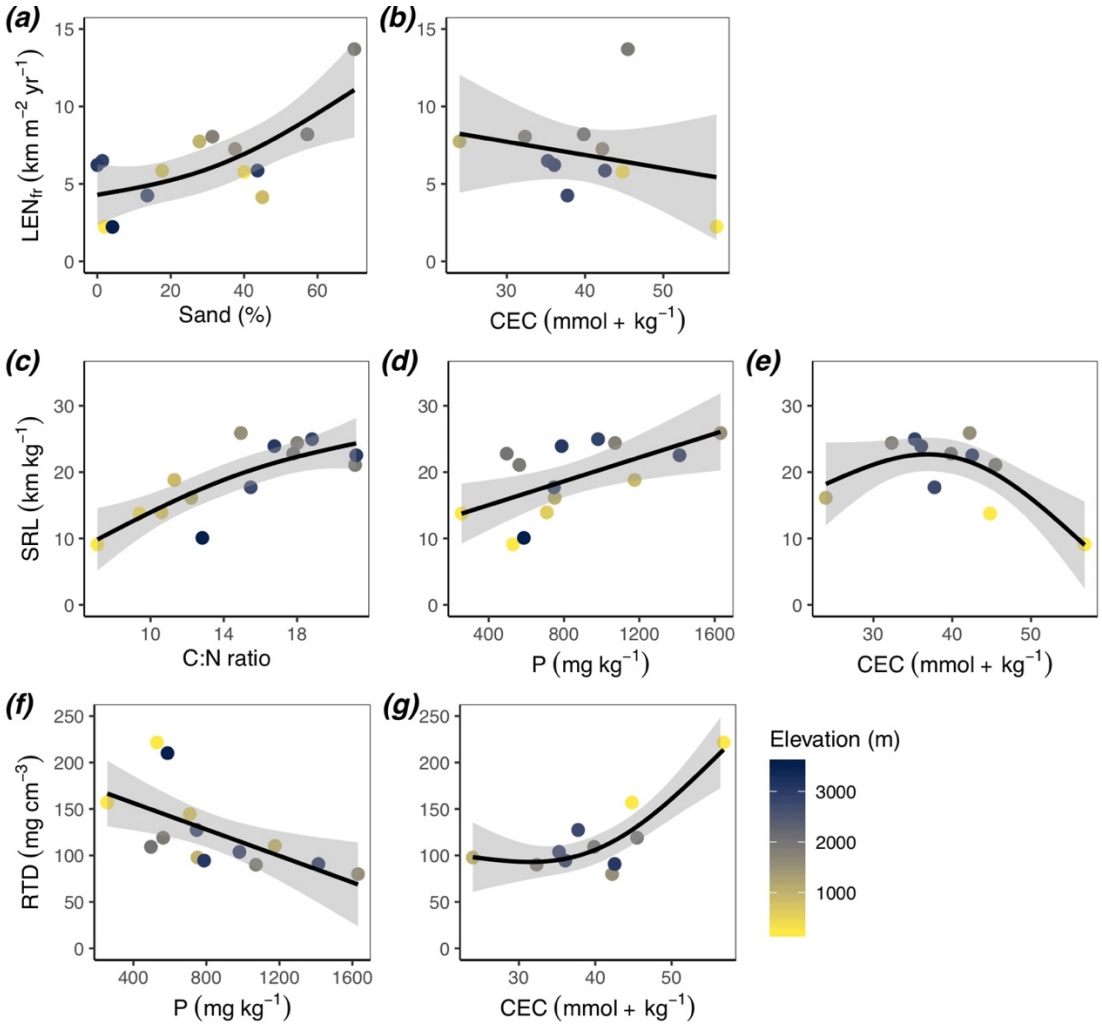


Figure 6.5. Generalised additive model (GAM) predictions of (a, b) fine root length growth (LEN_{fr}), (c, d, e) specific fine root length (SRL), and (f, g) fine root tissue density (RTD) in relation to total soil C:N ratio, sand content (%), soil phosphorus content (P, mg kg^{-1}), and cation exchange capacity (CEC, mmol+kg^{-1}). For model coefficients see Table 6.3. Continuous black lines indicate the GAM model predictions and grey bands show the 95% confidence intervals. Fine root morphological traits and soil properties are integrated over 0-30 cm soil depth. Each data point is a forest plot, coloured by elevation. The patterns in fine root surface area growth and specific fine root area were almost identical to those in LEN_{fr} and SRL, so they have been omitted for clarity.

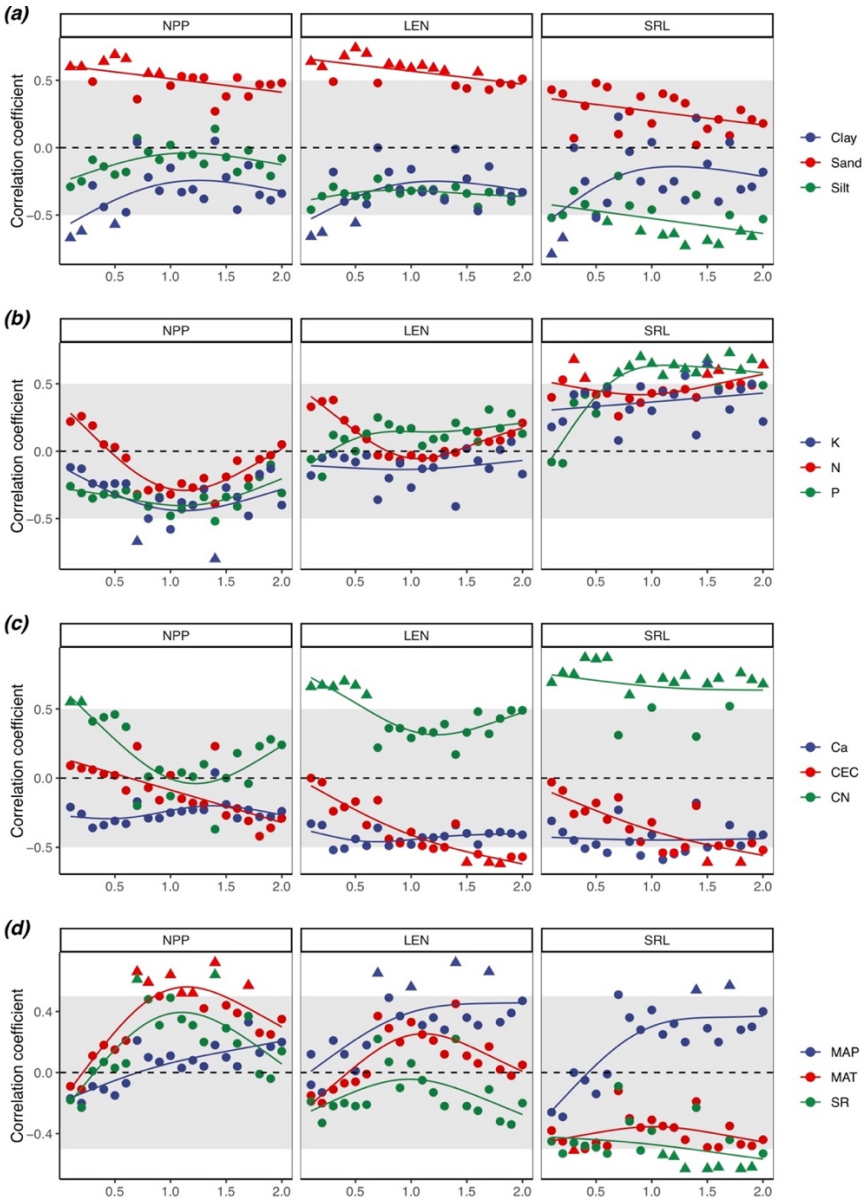


Figure 6.6. (a) Pearson correlation coefficients between root dynamic and morphological variables of fine root productivity (NPP_{fr}), fine root length growth (LEN_{fr}), and specific fine root length (SRL) in each 1 mm root diameter class, and edaphic and meteorological variables of (a) soil clay, silt and sand content, (b) soil N, P, and K content, (c) soil Ca content, CEC and C:N ratio, and (d) mean annual precipitation (MAP), mean annual temperature (MAT), and solar radiation (SR), calculated from the relationships between the root and environmental variables in question across the fifteen forest plots, separately for each diameter class. Triangles denote significant ($p < 0.05$) and dots non-significant correlations, respectively. The coloured lines are generalised additive model predictions with the correlation coefficient as the response variable and diameter class as explanatory variable. Horizontal black dashed lines at zero separate the negative and positive correlations and horizontal grey area shows correlation coefficients ± 0.5.

6.4 Discussion

6.4.1 Variation in fine root morphological traits and dynamics along the elevation gradient

Overall, our results revealed that fine root length and surface area growth peaked at mid-elevation, while fine root productivity did not vary with elevation. This seemingly contradictory result is explained by the variation in root tissue density which showed the opposite pattern to length and surface area growth, being at its lowest at mid elevation. At mid-elevations, plants invest in producing more root length, but these roots are lighter. As a result, the carbon investment remains similar.

The relationship between elevation and SRL and SRA almost exactly mirrored the pattern in length and surface area growth. The variation in SRL and SRA along the elevation gradient could be either due to the variation in root diameter distribution, variation in root tissue density, or some combination of the two. Our results show that almost all the variation in both SRL and SRA could be attributed to the variation in RTD, while the shifts in diameter distribution across the elevation gradient were small. Contrary to our results, a pantropical root trait study found a tight positive correlation between RTD and SRA, but not between RTD and SRL (Addo-Danso et al., 2020).

When we split the data into smaller diameter classes, the pattern in SRL and SRA along the elevation gradient was consistent across the size classes, showing a similar mid-elevation peak as the whole dataset, thus confirming that this pattern was not driven by a single size class. Fine root segments of 0.1-0.5 mm contributed proportionally more to the total root length growth in mid and high elevations than in low elevations (~60% vs. ~50%, respectively), while the reverse was true for larger diameter classes. This may indicate increased investment to small diameter absorptive roots at the expense of larger transport roots to increase the

efficiency of the uptake process as a response to poorer soils and colder temperatures, a strategy suggested e.g. by McCormack et al. (2015).

What causes this mid-elevation peak in root length growth, surface area growth, SRL and SRA (or trough, in case of RTD)? It is likely a combination of edaphic, climatic and biotic factors, which are not independent. The mid-elevation sites have high soil sand content and C:N ratio, and some sites have also low P content (Table 6.1, Figure S6.5), which according to our soil model explain a large proportion of the variation in root morphological traits. Mid elevation is also the cloud base zone, which is characterised by low solar radiation and low soil moisture (Malhi et al., 2017). It is also possible that the steep slope and the consequently dynamic soils in the mid-elevation sites favour these root traits.

The pattern may also be related to the tree species composition. These elevations are dominated by *Tachigali, Tapirira, Alchornea*, and *Miconia,* which are fast growing tree genera of low wood density (Farfan-Rios et al., 2015). According to the root economic spectrum hypothesis, fast-growing tree species have high SRL to enable rapid nutrient uptake (Weemstra et al., 2020). This has also been demonstrated in Afromontane forests in Ethiopia, where species with fast stem growth had higher SRL and SRA than species with slow stem growth (Assefa et al., 2018).

The high root length and surface area growth at mid-elevation may also indicate that tree species in those sites have fewer mycorrhizal fungal associations, therefore having to invest more into fine root growth to forage for nutrients and water. This is indirectly supported by the observation that the alpha diversity of fungal communities in the organic soil layer is the lowest at mid-elevation in this same transect (Nottingham et al., 2018). Furthermore, woody species with thinner roots and higher SRL have been shown to have lower colonisation levels of both arbuscular and ectomycorrhizal fungi (Comas et al., 2014).

Similar non-linear patterns with elevation have been previously reported in transects in Ecuador (Graefe et al., 2008) and Borneo (Okada et al., 2017; Ushio et al., 2015), where the relationship between elevation and root dynamic and morphological traits is driven by overlapping gradients of temperature and soil conditions.

6.4.2 Effect of soil properties and climatic variables on root morphological traits and dynamics

Soil properties explained a major proportion, between 71% to 86%, of the variability in root morphological traits and dynamics across the elevation gradient. Generalised additive models revealed that fine root morphological variables were driven by soil sand, C:N ratio, P, and CEC. Plants may have to compensate for the poorer nutrient and water holding capacity of sandy soils by investing more in root length and surface area growth. A similar effect of sand on root dynamics also was reported in lowland Malaysian Bornean rainforests, where LEN_{fr} and SA_{fr} growth were higher on sandy soil than on clay soil (Kochsiek et al., 2013).

The only soil variable that was a significant predictor for all root morphological traits and dynamics was cation exchange capacity, which had a negative relationship with LEN_{fr}, SA_{fr}, SRL, and SRA, but a positive relationship with RTD. These relationships indicate that when soil capacity to retain cations decrease (covarying with soil acidity, N content and P content), plants evoke strategies to increase soil nutrient uptake. A subtropical study reported that the addition of N decreased soil exchangeable K^+ and CEC in the top 10 cm of soil, and increased root biomass and root length (Fan et al., 2019).

Soil P was positively related to SRL and SRA, but was negatively related to RTD. A similar positive relationship between P and SRL (Addo-Danso et al., 2020; Hogan et al., 2020) and a similar negative relationship between P and RTD (Lugli et al., 2019) have been found in other tropical forest ecosystems as well. The increase in SRL and SRA is usually associated

with a decrease in root diameter on apical regions (Lambers et al., 2006), and under low soil P content, root absorptive area per surface area increases and residence time decreases (McCormack & Guo, 2014). SRL and SRA have been found to have a positive correlation with root phosphatase activity (Lugli et al., 2019; Okada et al., 2017), a key process in P mineralization. RTD is the trait that most consistently reflects adaptation to infertile soils and P limited systems (Holdaway et al., 2011; Kramer-Walter et al., 2016).

Soil C:N ratio had a positive relationship with SRL and SRA. C:N ratio also increased with increasing elevation and soil organic layer thickness, which has been reported in other montane forests as well (e.g. Germon et al., 2020; Graefe et al., 2008; Moser et al., 2010; Röderstein, Hertel, & Leuschner, 2005). Organic layer thickness may be one of the drivers of high SRL and SRA. As the organic layer is soft and the water content of the organic layer and mineral topsoil increases with elevation, light roots with high SRL may easily penetrate such soils (Malhi et al., 2017; Moser et al., 2010).

We gained new insights into how roots respond to soil properties and climatic variables by examining the root-environment relationships by individual root diameter classes, in addition to looking at fine roots as an entity. To our best knowledge, this is one of the first analyses of this kind for tropical forest ecosystems. As absorptive and transport roots have different functions, they may show different responses to environmental factors (Figure 6.6). The responses of fine root productivity, length and surface area growth, and SRL and SRA showed varying responses across diameter classes.

There was a significant positive correlation between soil sand content (and negative correlation between soil clay content) and NPP_{fr} and LEN_{fr} in the small diameter classes, but the correlation weakened towards larger diameter classes. These findings support the results

that sandy soils increase root absorptive area (Hendricks et al., 2006; Kochsiek et al., 2013), while indicating that soil texture may not be such an important control for the larger roots.

Fine root productivity and length growth did not correlate with soil nutrients, when examined by diameter classes. SRL and SRA increased with increasing soil P content, except for the smallest diameter classes. This apparent lack of relationship is probably due to the spatial scale of the sampling: the absorptive roots <0.6 mm diameter are likely to respond to the microscale variation of soil P, which our coarse-scale soil sampling does not capture.

Despite the large temperature (from 9.0 to 24.4℃, coefficient of variation 0.43) and precipitation (1560 to 5302 mm yr^{-1}, CV 0.29) gradients in our study, mean annual temperature and precipitation showed inconsistent and mostly non-significant relationships with root dynamics and traits across diameter classes. Solar radiation, despite its smaller variation (from 3.3 to 4.8 Gj m^{-2} yr^{-1}, CV 0.12), had a significant negative relationship with SRL and SRA in the larger diameter classes.

6.4.3 Conclusions

This study describes one of the largest tropical fine root morphological traits datasets, and presents data from fifteen elevations from lowland to upper montane forests. We report that almost all root morphological dynamics and traits peaked at mid-elevation montane forests, while root tissue density showed the opposite pattern. As a result of the opposite patterns in root length growth and root tissue density, root productivity did not vary along the elevation gradient. Our study highlights the importance of variation in root tissue density in determining root morphological traits and the rate of root foraging for resources. Considering root biomass production rates alone can miss the important variation in rates of resource foraging by roots, and important root-environment relationships.

Most of the variation in root morphological traits along the elevation gradient could be explained by the soil properties. One novel aspect of our study is the examination of the root-environment relationships by diameter classes, which showed varying patterns between smaller and larger fine roots. Fine root morphological traits respond to soil nutrients by increasing their external shape in sites with limited nutrient availability. Some of the variation may also be related to the species composition and tree growth rates. The next steps for increasing our understanding of root morphological traits should include species-level studies, sites across different geological soil formations and incorporation of mycorrhizal fungi into the research.

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6.6 References

Addo-Danso, S. D., Defrenne, C. E., Luke, E. D. M., Ostonen, I., Ernest, A. A., Kira, G. F., … Prescott, C. E. (2020). Fine-root morphological trait variation in tropical forest ecosystems : an evidence synthesis. *Plant Ecology*, *221*(1), 1–13. https://doi.org/10.1007/s11258-019-00986-1

Addo-Danso, S. D., Prescott, C. E., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Guy, R. D., … Malhi, Y. (2018). Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. *Biotropica*, *50*(4), 606–615. https://doi.org/10.1111/btp.12556

Andrade, E. M. De, Rosa, G. Q., Almeida, A. M. M. De, Silva, A. G. R. Da, & Sena, M. G. T. (2020). Rainfall regime on fine root growth in a seasonally dry tropical forest. *Revista Caatinga*, *33*(2), 458–469. https://doi.org/10.1590/1983-21252020v33n218rc

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Assefa, D., Godbold, D. L., Belay, B., Abiyu, A., & Rewald, B. (2018). Fine Root Morphology, Biochemistry and Litter Quality Indices of Fast- and Slow-growing Woody Species in Ethiopian Highland Forest. *Ecosystems*, *21*(3), 482–494. https://doi.org/10.1007/s10021-017-0163-7

Bartón, K. (2020). Multi-model inference, (1). ftp://xyz.csail.mit.edu/pub/CRAN/web/packages/MuMIn/MuMIn.pdf

Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I. M., & Roumet, C. (2014). Measurement of fine root tissue density: A comparison of three methods reveals the potential of root dry matter content. *Plant and Soil*, *374*(1–2), 299–313. https://doi.org/10.1007/s11104-013-1874-y

Comas, L. H., Callahan, H. S., & Midford, P. E. (2014). Patterns in root traits of woody species hosting arbuscular and ectomycorrhizas: implications for the evolution of belowground strategies. *Ecology and Evolution*, *4*(15), 2979–2990. https://doi.org/10.1002/ece3.1147

Eissenstat, D. M., Kucharski, J. M., Zadworny, M., Adams, T. S., & Koide, R. T. (2015). Linking root traits to nutrient foraging in arbuscular mycorrhizal trees in a temperate forest. *New Phytologist*, *208*(1), 114–124. https://doi.org/10.1111/nph.13451

Fan, Y., Zhong, X., Lin, F., Liu, C., Yang, L., Wang, M., … Yang, Y. (2019). Responses of soil phosphorus fractions after nitrogen addition in a subtropical forest ecosystem: Insights from decreased Fe and Al oxides and increased plant roots. *Geoderma*, *337*, 246–255. https://doi.org/10.1016/j.geoderma.2018.09.028

Farfan-Rios, W., Garcia-Cabrera, K., Salinas, N., Raurau-Quisiyupanqui, M. N., & Silman, M. R. (2015). Lista anotada de árboles y afines en los bosques montanos del sureste peruano: la importancia de seguir recolectando TT - An annotated checklist of trees and relatives in tropical montane forests from southeast Peru: the importance of continue collecting. *Revista Peruana de Biología*, *22*(2), 145–174. http://www.scielo.org.pe/scielo.php?script=sci_arttext&pid=S1727-99332015000200004&lang=pt

Freschet, G. T., Roumet, C., Comas, L. H., Weemstra, M., Bengough, A. G., Rewald, B., … Stokes, A. (2021). Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist*. https://doi.org/10.1111/nph.17072

Germon, A., Laclau, J.-P., Robin, A., & Jourdan, C. (2020). Tamm Review: Deep fine roots in

forest ecosystems: Why dig deeper? *Forest Ecology and Management*, *466*, 118135. https://doi.org/10.1016/j.foreco.2020.118135

Girardin, C. A. J., Aragão, L. E. O. C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D. B., Durand, L., … Whittaker, R. J. (2013). Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, *27*(1), 252–264. https://doi.org/10.1029/2011GB004082

Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., … Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*(12), 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x

Girardin, Cécile A.J., Espejo, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., … Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

Graefe, S., Hertel, D., & Leuschner, C. (2008). Fine root dynamics along a 2,000-m elevation transect in South Ecuadorian mountain rainforests. *Plant and Soil*, *313*(1–2), 155–166. https://doi.org/10.1007/s11104-008-9688-z

Harrell, F. E. (2020). Package "Hmisc," *4.4-2*, 1–405. https://hbiostat.org/R/Hmisc/, https://github.com/harrelfe/Hmisc/

Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., & Guo, D. (2006). Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *Journal of Ecology*, *94*(1), 40–57. https://doi.org/10.1111/j.1365-2745.2005.01067.x

Hogan, J. A., Valverde-Barrantes, O. J., Ding, Q., Xu, H., & Baraloto, C. (2020). Morphological variation of fine root systems and leaves in primary and secondary tropical forests of Hainan Island, China. *Annals of Forest Science*, *77*(3), 79. https://doi.org/10.1007/s13595-020-00977-7

Holdaway, R. J., Richardson, S. J., Dickie, I. A., Peltzer, D. A., & Coomes, D. A. (2011). Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology*, *99*(4), 954–963. https://doi.org/10.1111/j.1365-2745.2011.01821.x

Huaraca Huasco, W., Riutta, T., Girardin, C. A. J., Hancco Pacha, F., Puma Vilca, B. L., Moore, S., … Malhi, Y. (2021). Fine root dynamics across pantropical rainforest ecosystems. *Global Change Biology*, *27*(15), 3657–3680. https://doi.org/10.1111/gcb.15677

Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., … Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist*, *215*(1), 15–26. https://doi.org/10.1111/nph.14486

Kassambara, A., & Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. Package Version 1.0.7. *R Package Version*. https://cran.r-project.org/web/packages/factoextra/factoextra.pdf

Kochsiek, A., Tan, S., & Russo, S. E. (2013). Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology*, *214*(6), 869–882. https://doi.org/10.1007/s11258-013-0215-9

Kong, D., Wang, J., Wu, H., Valverde-barrantes, O. J., Wang, R., Zeng, H., … Feng, Y. (2019). Nonlinearity of root trait relationships and the root economics spectrum. *Nature Communications*, *10*(1), 1–9. https://doi.org/10.1038/s41467-019-10245-6

Kong, D., Wang, J., Zeng, H., Liu, M., Miao, Y., Wu, H., & Kardol, P. (2017). Letter The nutrient absorption – transportation hypothesis : optimizing structural traits in absorptive roots. *New Phytologist*, *213*(4), 1569–1572. https://doi.org/10.1111/nph.14344

Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., & Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology*, *104*(5), 1299–1310. https://doi.org/10.1111/1365-2745.12562

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J., & Veneklaas, E. J. (2006). Root Structure and Functioning for Efficient Acquisition of Phosphorus: Matching Morphological and Physiological Traits. *Annals of Botany*, *98*(4), 693–713. https://doi.org/10.1093/aob/mcl114

Lugli, L. F., Andersen, K. M., Aragão, L. E. O. C., Cordeiro, A. L., Cunha, H. F. V., Fuchslueger, L., … Hartley, I. P. (2019). Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil*, *450*(1–2), 49–63. https://doi.org/10.1007/s11104-019-03963-9

Makita, N., Kosugi, Y., Dannoura, M., Takanashi, S., Niiyama, K., Kassim, A. R., & Nik, A. R. (2012). Patterns of root respiration rates and morphological traits in 13 tree species in a tropical forest. *Tree Physiology*, *32*(3), 303–312. https://doi.org/10.1093/treephys/tps008

Malhi, Y., del Aguilla-Pasquell, J., Metcalfe, D. B., Phillips, O. L., Farfan-Rios, W., Silman, M., … Farfán Amézquita, F. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Marthews, T. R., Riutta, T., Menor, I. O., Urrutia, R., Moore, S., Metcalfe, D., … Networks, C. R. and colleagues from the R. and G. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0, 121.

McCormack, M. L., Dickie, I. A., Eissenstat, D. M., Fahey, T. J., Fernandez, C. W., Guo, D., … Zadworny, M. (2015). Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *The New Phytologist*, *207*(3), 505–518. https://doi.org/10.1111/nph.13363

McCormack, M. L., & Guo, D. (2014). Impacts of environmental factors on fine root lifespan. *Frontiers in Plant Science*, *5*, 205. https://doi.org/10.3389/fpls.2014.00205

McCormack, M. L., Guo, D., Iversen, C. M., Chen, W., Eissenstat, D. M., Fernandez, C. W., … Zanne, A. (2017). Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytologist*, *215*(1), 27–37. https://doi.org/10.1111/nph.14459

McCormack, M. L., & Iversen, C. M. (2019). Physical and Functional Constraints on Viable Belowground Acquisition Strategies. *Frontiers in Plant Science*, *10*, 1215. https://doi.org/10.3389/fpls.2019.01215

Metcalfe, D. B., Williams, M., Aragão, L. E. O. C., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., … Meir, P. (2007). A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. *New Phytologist*, *174*(3), 697–703. https://doi.org/10.1111/j.1469-8137.2007.02032.x

Metcalfe, Daniel B., Meir, P., Aragão, L. E. O. C., da Costa, A. C. L., Braga, A. P., Gonçalves, P. H. L., … Williams, M. (2008). The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil*, *311*(1–2), 189–199.

https://doi.org/10.1007/s11104-008-9670-9
Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., & Hertel, D. (2010). Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. *Plant Ecology & Diversity*, *3*(2), 151–164. https://doi.org/10.1080/17550874.2010.517788
Nottingham, A. T., Fierer, N., Turner, B. L., Whitaker, J., Ostle, N. J., McNamara, N. P., … Meir, P. (2018). Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. *Ecology*, *99*(11), 2455–2466. https://doi.org/10.1002/ecy.2482
Okada, K., Aiba, S., & Kitayama, K. (2017). Influence of temperature and soil nitrogen and phosphorus availabilities on fine-root productivity in tropical rainforests on Mount Kinabalu, Borneo. *Ecological Research*, *32*(2), 145–156. https://doi.org/10.1007/s11284-016-1425-0
Quesada, C. A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T. R., Czimczik, C., … Paiva, R. (2009). Chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences Discussions*, *6*(2), 3923–3992. https://doi.org/10.5194/bgd-6-3923-2009
Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. *Journal of Ecology*, *102*(2), 275–301. https://doi.org/10.1111/1365-2745.12211
Röderstein, M., Hertel, D., & Leuschner, C. (2005). Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology*, *21*(5), 483–492. https://doi.org/10.1017/S026646740500249X
Rowland, L., Malhi, Y., Silva-Espejo, J. E., Farfán-Amézquita, F., Halladay, K., Doughty, C. E., … Phillips, O. L. (2014). The sensitivity of wood production to seasonal and interannual variations in climate in a lowland Amazonian rainforest. *Oecologia*, *174*(1), 295–306. https://doi.org/10.1007/s00442-013-2766-9
Sierra Cornejo, N., Hertel, D., Becker, J. N., Hemp, A., & Leuschner, C. (2020). Biomass, Morphology, and Dynamics of the Fine Root System Across a 3,000-M Elevation Gradient on Mt. Kilimanjaro. *Frontiers in Plant Science*, *11*, 13. https://doi.org/10.3389/fpls.2020.00013
Silver, W. L., Thompson, A. W., McGroddy, M. E., Varner, R. K., Dias, J. D., Silva, H., … Keller, M. (2005). Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Global Change Biology*, *11*(2), 290–306. https://doi.org/10.1111/j.1365-2486.2005.00903.x
Ushio, M., Fujiki, Y., Hidaka, A., & Kitayama, K. (2015). Linkage of root physiology and morphology as an adaptation to soil phosphorus impoverishment in tropical montane forests. *Functional Ecology*, *29*(9), 1235–1245. https://doi.org/10.1111/1365-2435.12424
Wang, R., Wang, Q., Liu, C., Kou, L., Zhao, N., Xu, Z., … He, N. (2018). Changes in trait and phylogenetic diversity of leaves and absorptive roots from tropical to boreal forests. *Plant and Soil*, *432*(1–2), 389–401. https://doi.org/10.1007/s11104-018-3816-1
Weemstra, M., Kiorapostolou, N., Ruijven, J., Mommer, L., Vries, J., & Sterck, F. (2020). The role of fine-root mass, specific root length and life span in tree performance: A whole-tree exploration. *Functional Ecology*, *34*(3), 575–585. https://doi.org/10.1111/1365-2435.13520
Wood, S. (2019). *Package 'mgcv.' Version 1.8-29*. https://doi.org/10.1201/9781315370279
Wurzburger, N., & Wright, S. J. (2015). Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology*, *96*(8), 2137–2146. https://doi.org/10.1890/14-1362.1

6.7 Supplementary material

Supplementary tables

Table S6.1 Loadings of the soil variables on the first four axes of the Principal Component Analysis (PCA) from lowland forests to montane forests (see Figure S6.1). The highest loading on each axis is shown in bold. EV is the error or proportion of variance.

Soil properties	PC1 EV (0.34)	PC2 EV (0.22)	PC3 EV (0.14)	PC4 EV (0.09)
Sand	0.08	0.45	**0.52**	0.22
Silt	-0.39	-0.14	0.02	0.23
Clay	-0.12	-0.39	-0.23	0.48
N	0.40	-0.22	-0.11	-0.21
CN	**0.43**	0.00	0.35	-0.09
P	0.18	**-0.47**	0.47	0.05
K	0.34	-0.35	-0.22	-0.31
Mg	-0.20	-0.42	0.49	0.10
Ca	-0.44	-0.22	-0.08	-0.39
CEC	-0.32	0.09	0.17	**-0.60**

Supplementary figures

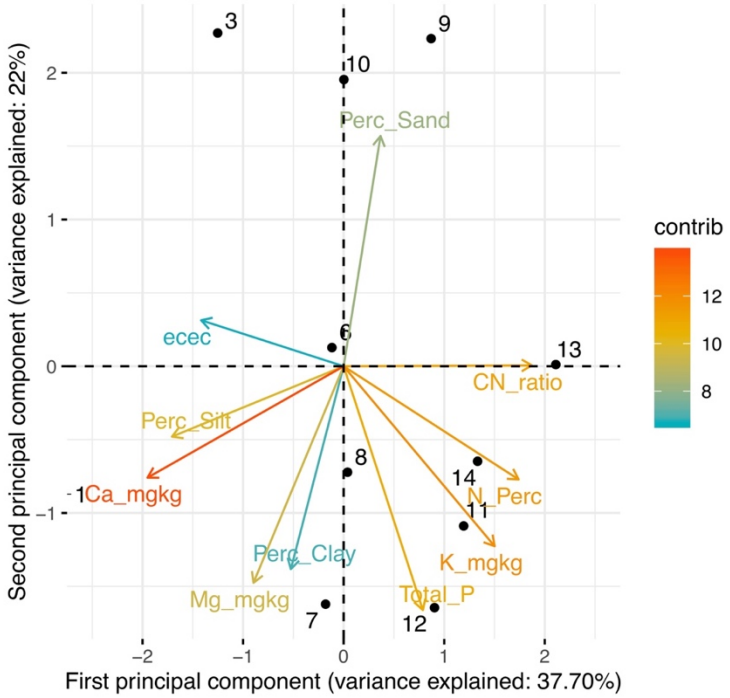


Figure S6.1. Principal Component Analysis (PCA) of plot-level (n=15) soil properties across the Andean montane forests transect.

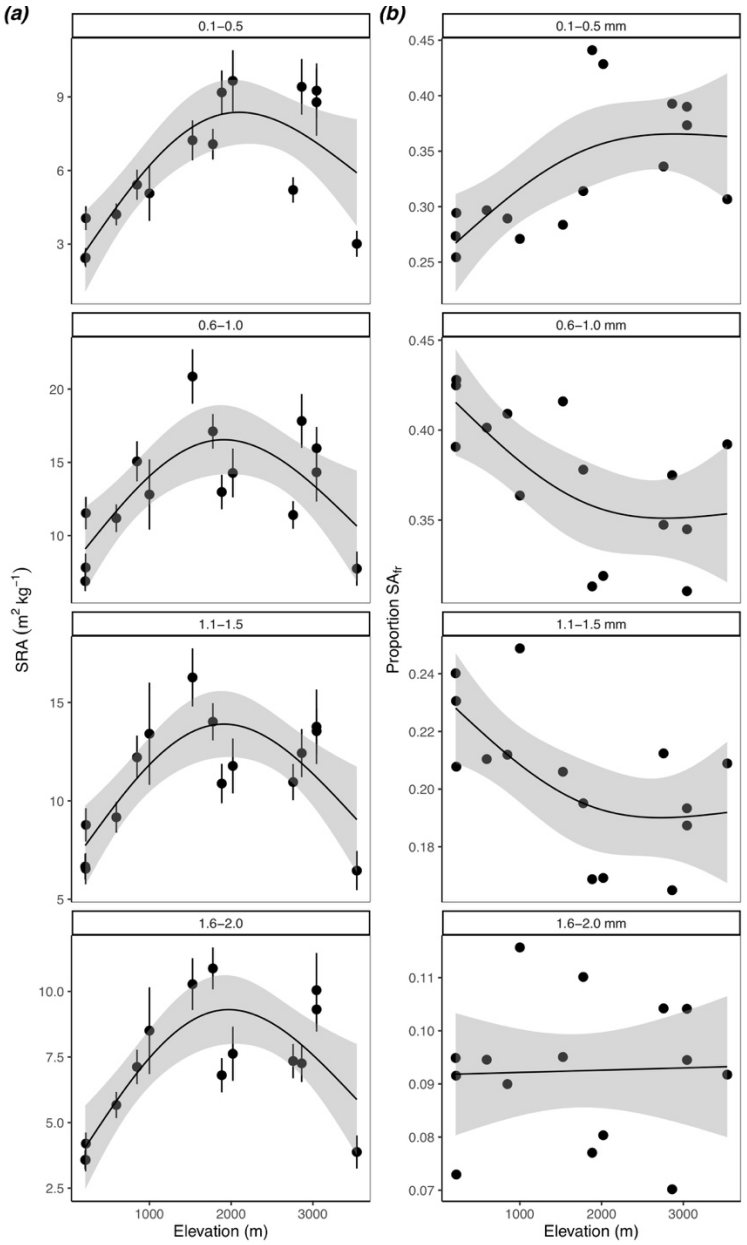


Figure S6.2. Relationship between elevation and (a) specific fine root area (SRA, m^2 kg^{-1}) by root diameter classes and (b) the proportional contribution of each diameter class to total fine root surface area growth (SA_{fr}). Continuous black lines are the generalised additive model predictions grey bands show the 95% confidence interval for the predictions. Error bars are standard errors of the mean.

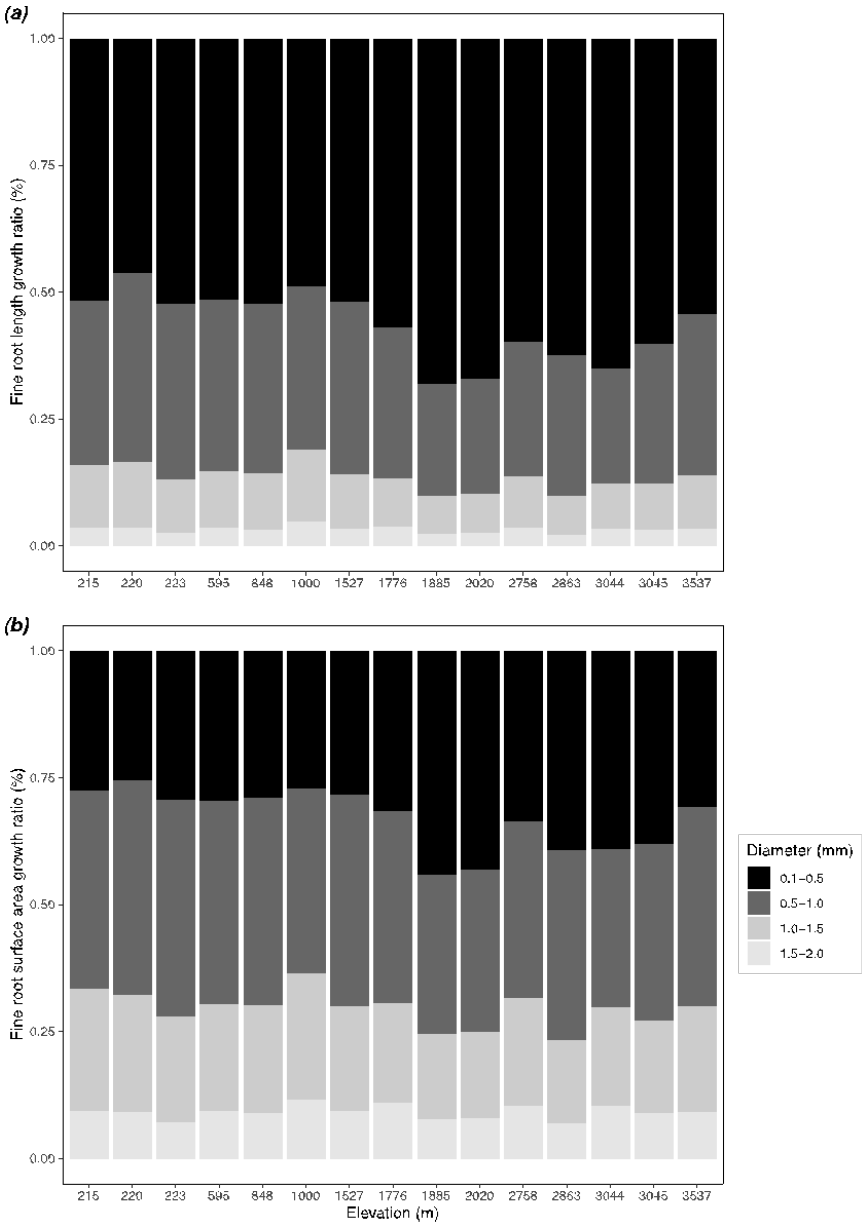


Figure S6.3 Fractional contribution (%) of each 0.5 mm fine root diameter class to the total (a) fine root length growth and (b) surface area growth along the elevation gradient.

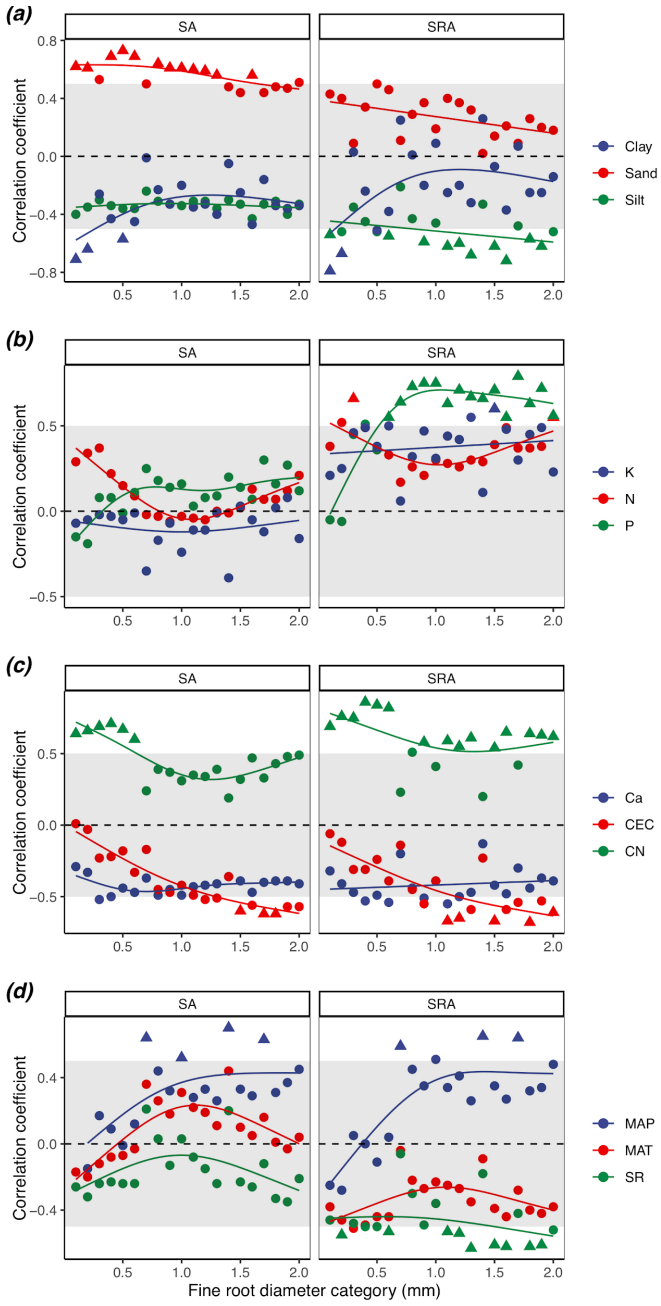


Figure S6.4. Pearson correlation coefficients between fine root morphological traits (surface area growth and specific root area) in each 1 mm root diameter class, and edaphic and meteorological variables of (a) soil clay, silt and sand content, (b) soil N, P, and K content, (c) soil Ca content, CEC and C:N ratio, and (d) mean annual precipitation (MAP), mean annual temperature (MAT), and solar radiation (SR), calculated from the relationships between the variables in question across the fifteen forest plots. Triangles denote significant ($p < 0.05$) and dots non-significant correlations, respectively. The coloured lines are generalised additive model predictions. Horizontal black dashed lines at zero separate the negative and positive correlations and horizontal grey area shows Pearson correlation coefficients ± 0.5.

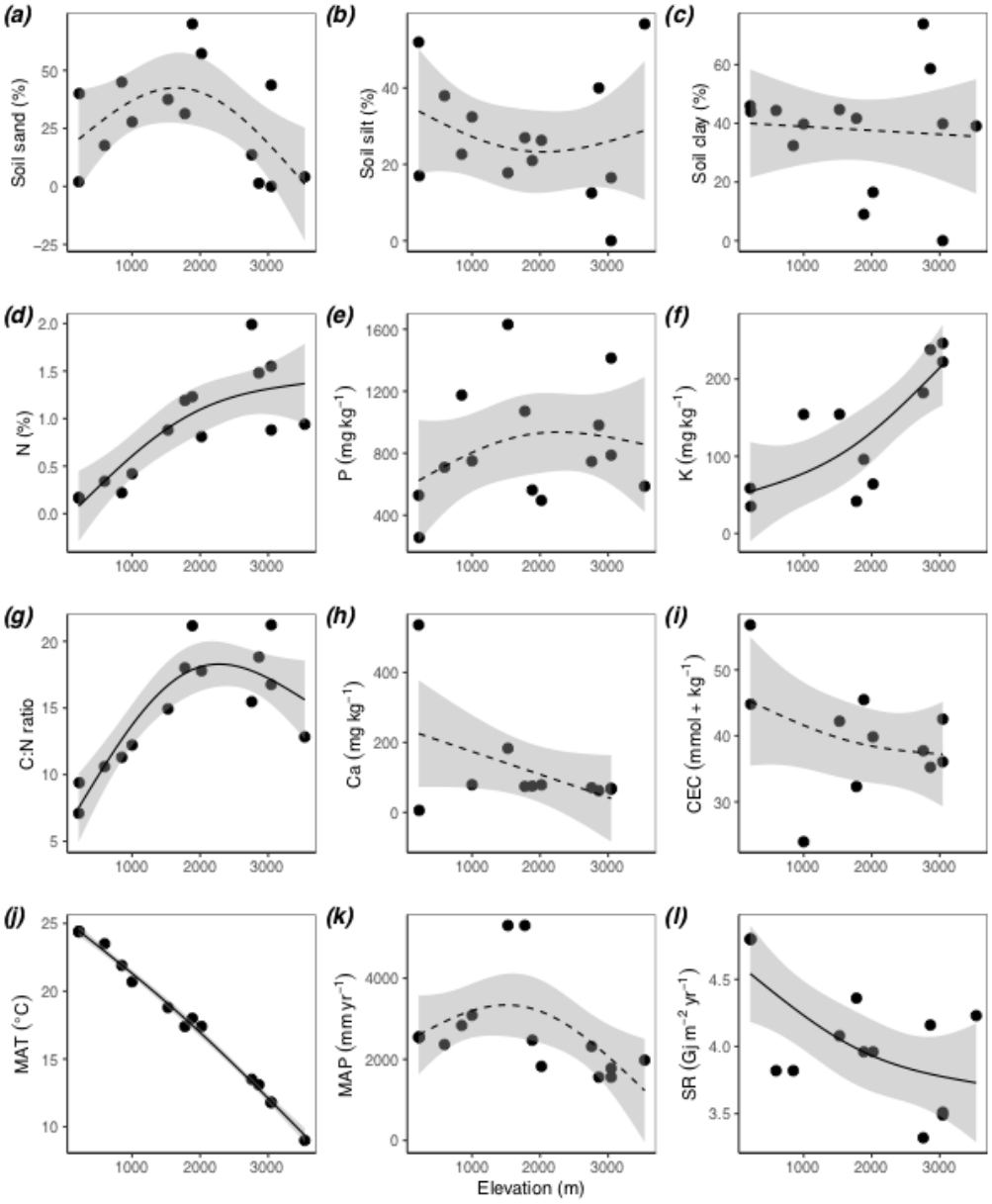


Figure S6.5. Generalised additive model (GAM) predictions of soil properties and climate variables along the elevation gradient from lowland to upper montane forests. The black lines are GAM predictions (continuous lines - significant; dashed lines - not significant) and the grey band is the 95% confidence interval of the predictions.

Chapter 7: General discussion

7.1 Key findings

This last section of my thesis summarises how my study has addressed the general questions established in Chapter 1 (section 1.2). In the process of conducting this thesis research I have synthesised and analysed the largest fine root dynamics and morphological traits studies at regional and global scales in old-growth tropical forest ecosystems of South America, Africa, and Southeast Asia.

7.1.1 What are the common environmental factors that explain fine root dynamics, and is there a single unified model of fine root dynamics across tropical forest ecosystems?

In my first data chapter (Chapter 4), I reported that fine root carbon stock, productivity, residence time, and fractional allocation of total net primary productivity to the fine roots vary across sites in lowland and montane forest ecosystems (Figure 7.1). A different set of environmental factors explain this variation in lowland and montane forests. In lowland forests, the variation in fine root carbon stock and dynamics is driven by soil chemistry and physics, rather than by climate. In montane forests, climatic factors explain some of the variation in root dynamics, although edaphic factors still dominate (Figure 7.1).

I observed high fine root carbon stocks across lowland forests in the parts of the of humid Amazon forest region and low fine root carbon stocks in Dipterocarp-dominated old-growth forests (Malaysian Borneo) and in dry deciduous forests (Brazil). In montane forests, the highest fine root carbon stocks were found at mid-elevation. Fine root carbon stock is a good predictor of fine root productivity in lowland forests but not in montane forests (Chapter 4, Figure 4.3). In Chapter 5, I showed that fine root productivity estimates recorded with ingrowth core and rhizotron techniques are fairly consistent in lowland forests. However, this

close correspondence breaks down in montane forests because fine root productivity may be underestimated with the ingrowth core technique (Chapter 5, Figure 5.2). The apparent decline in fine root productivity with increasing elevation may be related to this underestimation of root productivity in montane forests by widely used ingrowth core techniques, mainly from mid-elevation to treeline forests. I suggest this underestimation is due to the large disturbance caused by the installation and the three-monthly harvest on these fragile soils and to the contraction and expansion of highly organic soil inside the core between dry and wet periods, which disturbs root growth. I found that the strongest driver of fine root productivity is soil sand content in lowland forests and mean annual temperature in montane forests. In addition, soil sand content is an even more strong driver of fractional carbon allocational of total net primary productivity to the fine roots in lowland forests. In montane forests, on the other hand, root fractional allocation of total net primary productivity is negatively related to soil phosphorus content (Chapter 4, Figure 4.4).

Fine root residence time is related to multiple environmental variables, with a positive relationship with soil sand content and soil acidity in lowland forests. In montane forest, root residence time increases with increasing soil nitrogen content (Chapter 4, Figure 4.4) and elevation (Chapter 5, Figure 5.6). Across the forest type, I found a positive relationship between residence time and specific root length (Chapter 6, Figure 6.4).

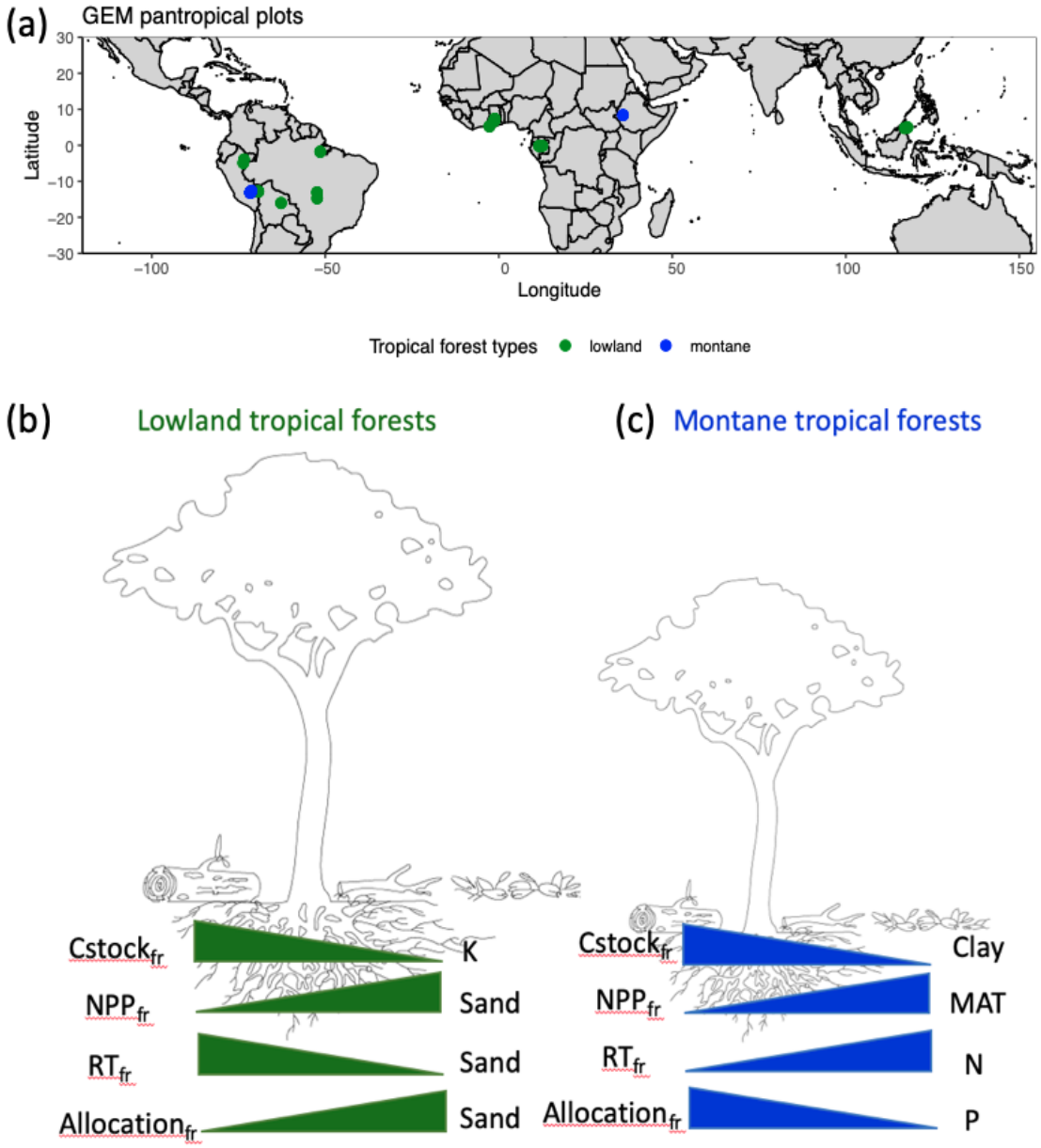


Figure 7.1. (a) Location of GEM plots in lowland (green dots) and montane (blue dots) tropical forest ecosystems. Significant root - environment relationships in (b) lowland forest and (c) montane forests. $Cstock_{fr}$ - fine root carbon stock, NPP_{fr} -fine root productivity, RT_{fr} - fine root residence time, $Allocation_{fr}$ - fractional allocation of total net primary productivity to fine roots; K - soil potassium content, Sand - soil sand content, Clay - soil clay content, MAT - mean annual temperature, N - soil nitrogen content, P - soil phosphorus content.

7.1.2 How does fine root productivity and mortality vary both seasonally and vertically along the soil profile in Amazonian and Andean forests?

Chapter 5 examined how the soil depth distribution and seasonal variation of fine root productivity, mortality, and residence time vary in lowland Amazon and Andean montane forests. The deployment of screen rhizotrons enabled a unique analysis of vertical profiles in root dynamics, and also a high temporal resolution analysis of root growth and mortality. I observed that fine root carbon stock and soil organic layer thickness are positively correlated in montane forests. In lowland and pre-montane forests over 50% of fine root carbon stock is stored in the top 10 cm soil depth. I found that the steepness of the vertical profile of fine root productivity decreases with increasing elevation and with soil organic layer thickness (Figure 5.5), and root residence time increases with increasing elevation, but does not show a clear vertical pattern with soil depth (Figure 5.6).

Seasonal variation of root productivity and mortality is driven by precipitation. In lowland Amazonia, mortality exceeds productivity in the dry season. In montane forests, root productivity peaks in the dry season and root mortality peaks both in the rainy and dry seasons. These high temporal resolution results would not have been possible to obtain with the ingrowth core method, which requires longer collection intervals so that enough roots accumulate. Hence, this study highlights the advantages of the rhizotron technique in understanding the monthly variation of fine root productivity. Furthermore, rhizotrons are an effective tool for recording mortality, and partitioning the productivity and mortality data by soil depth layers.

7.1.3 How are fine root morphological traits affected by soil nutrient content and environmental factors across different root diameter categories?

The last empirical chapter (Chapter 6) of my thesis reports fine root morphological traits from lowland Amazon to Andean upper montane forests and examines their relationships with soil

properties, climatic factors, and root carbon dynamics. I observed that the mean annual fine root length and surface area growth, specific root length and specific surface area peak at mid-elevation in montane forests (Figure 6.1). In contrast, I found that root tissue density shows a trough at mid-elevation. Hence, a key finding is that morphological dynamics (rate of growth of root area and length) are not strongly related to root productivity (Figure 6.4), because of the variation in root tissue density. Fine root productivity did not vary along the elevation gradient, indicating similar carbon investment across sites. The fact that root morphological dynamics and traits did vary indicates that different plant communities employ different root strategies for the same unit carbon cost. Root tissue density emerged as the main variable in determining root morphological and dynamic traits. These results also show that root morphological traits are poor predictors of root carbon dynamics (but good predictors of morphological dynamics).

Figure 7.2 shows the key root and soil relationships along the elevation gradient. Root morphological traits respond to soil nutrients by changing their external shape under limited soil nutrient availability. I show that fractional allocation of total net primary productivity to fine roots (Figure 4.4) and fine root tissue density (Figure 6.5) are strongly related to soil P content in montane forests. These relationships are not invariant across root diameter classes, however. The novel analysis in Chapter 6 shows that the smallest roots, which are likely to be the first-order absorptive roots, are related to a different set of variables than the larger transport roots (Figure 6.6, Figure 7.1, Figure 7.2).

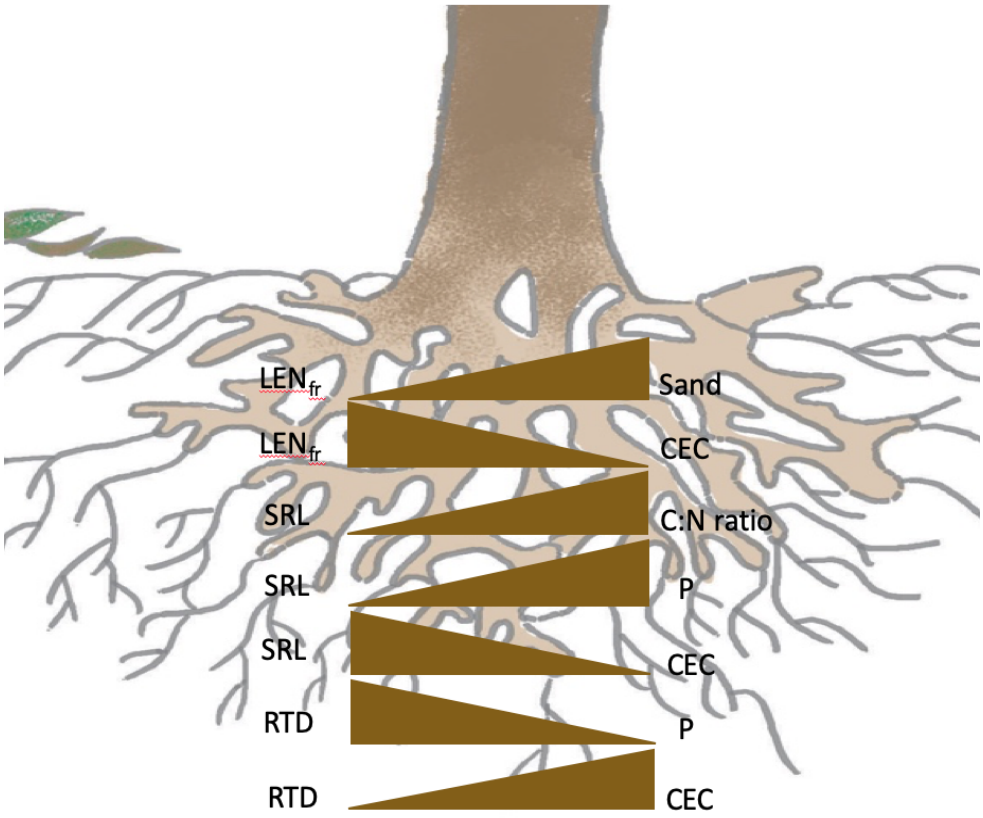


Figure 7.2. Fine root morphological dynamics and traits relationship with soil sand content (Sand), cation exchange capacity (CEC), carbon-nitrogen ratio (C:N), phosphorus content (P) from lowland to upper montane forest ecosystems. Dynamics include fine root length production (LEN_{fr}), and traits include specific fine root length (SRL), and fine root tissue density (RTD).

7.2 Implications for tropical lowland and montane forests ecosystems

Globally, fine root carbon stock and productivity are higher in tropical forests than in temperate and boreal forests (Finér et al., 2011; Wang et al., 2018). However, how these features are related to highly varied soil properties and climatic variables across the tropical forest ecosystems remains unclear. These relationships are crucial to understand the aboveground and belowground carbon cycles in old-growth forests and how ecosystem changes might disrupt the current patterns of root carbon dynamics. Chapter 4 of my thesis has implications for understanding and modelling of regional and global carbon storage and fluxes, to increase the accuracy of quantification and modelling of fine root carbon stock, productivity, residence

time, and fractional allocation of total primary productivity to the fine roots. In addition, this thesis reveals that relationships between fine root dynamics and soil properties and climatic variables are different between montane and lowland forests.

The importance of soil moisture and water availability as drivers of the seasonal variation of fine root productivity and mortality in tropical forests is well known. However, a novel result of this study, the increase of productivity during the dry seasons and increase of root mortality during the rainy season in montane forests, is still poorly understood. I hypothesise that high fine root productivity in the dry season compensates for high mortality events in the rainy season in montane forests where plants grow in waterlogged soils. In addition, autotrophic soil respiration is lower montane forests in the rainy season of January, February, and March (Girardin et al., 2014; Huaraca Huasco et al., 2014), and this indicates that root productivity is lower in the rainy season than dry season in montane forests.

My study on fine root morphological dynamics and traits in tropical lowland and montane forests highlighted the divergent relationship of different-sized roots with soil properties and climatic variables. The pattern between elevation and root morphological dynamics and traits is not linear. The peak in root morphological dynamics and traits at mid-elevation are driven by soil properties and covarying tree community composition. These forests are frequently covered by cloud and theses altitude is highly susceptibility to landslides (Clark et al., 2016), where the mean annual precipitation is higher than pre and upper montane forests (Huaraca Huasco et al., 2014; Rapp & Silman, 2012).

A practical implication of my research is to recommend screen rhizotrons as a cost-effective method for estimating root productivity and mortality. In particular, rhizotrons may perform better than ingrowth cores in fragile, organic, and waterlogged soils, and in sites with slow root turnover rate. For such sites, many of the estimates presented in the current literature (collected using ingrowth cores) may need to be revised.

7.3 Future research topics and directions

There are several research topics to carry out to increase our understanding of the belowground carbon cycle in tropical forest ecosystems. In the next paragraphs, I list some important research topics for future studies.

First, increasing the number studies of whole system NPP and hence of fractional carbon allocation to the fine roots will help us understand the relationships between belowground and aboveground carbon allocation and their relationships with soil properties, climatic variables, and plant functional traits. Understanding root carbon allocation in the context of whole ecosystem carbon dynamics adds a great values and insight that is not possible when root dynamics are considered in isolation. In addition, monitoring seasonal variation of fine root productivity, mortality, and allocation together with monthly variation in precipitation and water deficit across tropical forests may help us understand the effect of severe drought events on ecosystem carbon dynamics.

Second, soil depth distribution of fine root carbon stock, productivity, mortality, and residence time is poorly understood. However, the latest studies showed that ~50% of fine root productivity is produced below 30 cm depth and fine root carbon stock increased in dry periods in the deep soil layers where water availability is higher (Cordeiro et al., 2020). Seedlings growth experiment of African moist forests, dry forests, transition zone, humid savanna, and dry savanna tree species revealed that root mass fraction, mean rooting depth, and specific root length increased with decreasing mean annual precipitation from wet forests to dry savanna forests (Boonman et al., 2020). In addition, deep rooting in tropical forests is related to soil groundwater, although this relationship remains unclear in many tropical regions due to a lack of data (Fan et al., 2017; Zhou et al., 2020). Therefore, the deep soil carbon cycle is a key gap

in our understanding, not only of root carbon stocks, but also root productivity, residence time, allocation, and morphological traits.

Third, root morphological dynamics and traits are key features determining the uptake of soil nutrients, yet their relationship to soil properties and climatic factors has been poorly studied in tropical forests. There is a need for studies on root morphological traits at different diameter classes at the species level in tropical forest ecosystems to improve the understanding of the plant economic spectrum.

Finally, combined effect of the rising atmospheric CO_2, temperature, and increased frequency of drought events have resulted in a net decline in the carbon sink in African and Amazon forests, with highest impact in the hottest tropical regions (Hubau et al., 2020; Sullivan et al., 2020). Rising CO_2 concentration and temperatures are likely to change the fractional allocation of total net primary productivity to the fine roots (Piñeiro et al., 2020; Warren et al., 2015). However, the climate change impact on fine root dynamics and morphological traits and the changes in soil nutrient demand and water uptake remain poorly understood across old-growth and logged tropical forests. Such information will help improve future understanding on forest carbon stocks and dynamics, and will inform programs of tropical ecosystem restoration and conservation.

In conclusion, I believe this pantropical study has yielded substantial new insight and advances in both the methodology and understanding of tropical forest root dynamics, but also opens up a number of new questions and challenges.

7.4 References

Boonman, C. C. F., van Langevelde, F., Oliveras, I., Couédon, J., Luijken, N., Martini, D., & Veenendaal, E. M. (2020). On the importance of root traits in seedlings of tropical tree species. *New Phytologist*, *227*(1), 156–167. https://doi.org/10.1111/nph.16370

Clark, K. E., West, A. J., Hilton, R. G., Asner, G. P., Quesada, C. A., Silman, M. R., … Malhi, Y. (2016). Storm-triggered landslides in the Peruvian Andes and implications for topography, carbon cycles, and biodiversity. *Earth Surface Dynamics*, *4*(1), 47–70. https://doi.org/10.5194/esurf-4-47-2016

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde-Barrantes, O., Fuchslueger, L., Oblitas, E., … Quesada, C. A. (2020). Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. *Plant-Environment Interactions*, *1*(1), 3–16. https://doi.org/10.1002/pei3.10010

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(40), 10572–10577. https://doi.org/10.1073/pnas.1712381114

Finér, L., Ohashi, M., Noguchi, K., & Hirano, Y. (2011). Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management*, *262*(11), 2008–2023. https://doi.org/10.1016/j.foreco.2011.08.042

Gatti, L. V., Basso, L. S., Miller, J. B., Gloor, M., Domingues, L. G., Cassol, H. L. G., … Neves, R. A. L. (2021). Amazonia as a carbon source linked to deforestation and climate change. *Nature*, *595*. https://doi.org/10.1038/s41586-021-03629-6

Girardin, C. A. J., Espejo, J. E. S., Doughty, C. E., Huasco, W. H., Metcalfe, D. B., Durand-Baca, L., … Malhi, Y. (2014). Productivity and carbon allocation in a tropical montane cloud forest in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 107–123. https://doi.org/10.1080/17550874.2013.820222

Hubau, W., Lewis, S. L., Phillips, O. L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., … Zemagho, L. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature*, *579*(7797), 80–87. https://doi.org/10.1038/s41586-020-2035-0

Huaraca Huasco, W., Girardin, C. A. J., Doughty, C. E., Metcalfe, D. B., Baca, L. D., Silva-Espejo, J. E., … Malhi, Y. (2014). Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, *7*(1–2), 125–142. https://doi.org/10.1080/17550874.2013.819042

Piñeiro, J., Ochoa-Hueso, R., Drake, J. E., Tjoelker, M. G., & Power, S. A. (2020). Water availability drives fine root dynamics in a Eucalyptus woodland under elevated atmospheric CO2 concentration. *Functional Ecology*, *34*(11), 2389–2402. https://doi.org/10.1111/1365-2435.13660

Rapp, J., & Silman, M. (2012). Diurnal, seasonal, and altitudinal trends in microclimate across a tropical montane cloud forest. *Climate Research*, *55*(1), 17–32. https://doi.org/10.3354/cr01127

Sullivan, M. J. P., Lewis, S. L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A. C., … Phillips, O. L. (2020). Long-term thermal sensitivity of Earth's tropical forests. *Science*, *368*(800), 869–874. Retrieved from 10.1126/science.aaw7578

Wang, C., Chen, Z., Brunner, I., Zhang, Z., Zhu, X., Li, J., … Li, M.-H. (2018). Global patterns of dead fine root stocks in forest ecosystems. *Journal of Biogeography*, *45*(6), 1378–1394. https://doi.org/10.1111/jbi.13206

Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., & Wullschleger, S. D. (2015). Root structural and functional dynamics in terrestrial biosphere models - evaluation and recommendations. *New Phytologist*, *205*(1), 59–78. https://doi.org/10.1111/nph.13034

Zhou, Y., Wigley, B. J., Case, M. F., Coetsee, C., & Staver, A. C. (2020). Rooting depth as a key woody functional trait in savannas. *New Phytologist*, *227*(5), 1350–1361. https://doi.org/10.1111/nph.16613