New Phytologist

Tansley review
Plant phosphorus-use and -acquisition strategies in Amazonia

Tatiana Reichert[1], Anja Rammig[1], Lucia Fuchslueger[2], Laynara F. Lugli[3], Carlos A. Quesada[3], Katrin Fleischer[4,1]

[1] Technical University of Munich, School of Life Sciences, Freising, Germany, 85354

[2] University of Vienna, Centre of Microbiology and Environmental Systems Science, Vienna, Austria, 1090

[3] National Institute of Amazonian Research, Manaus, Brazil, 69060-062

[4] Max Planck Institute for Biogeochemistry, Department Biogeochemical Signals, Jena, Germany, 07745

Article acceptance date: 20 December 2021

Supporting information

Contents

Notes S1. Leaf P_i-resorption efficiency

Leaf P_i-resorption efficiency is an essential metric for dynamic vegetation models (Fleischer *et al.*, 2019); it is defined as the percentage of remobilized nutrients in fully senesced leaves compared with those in mature green leaves (Van Heerwaarden *et al.*, 2003; Killingbeck, 2004). However, the relationship between leaf P_i-resorption efficiency and soil P availability is still ambiguous due to contrasting observations. Various field studies and meta-analyses have shown a robust negative relationship between P_i-resorption efficiency and soil P concentrations (Yuan & Chen, 2009; Hidaka & Kitayama, 2011; Han *et al.*, 2013; Hayes *et al.*, 2014; Tsujii *et al.*, 2017; Wang *et al.*, 2018; He *et al.*, 2020), while others showed weak or no relationships (Aerts, 1996; Vitousek, 1998; Aerts & Chapin III, 1999; Eckstein *et al.*, 1999; Wright & Westoby, 2003; Tang *et al.*, 2013). This controversy might have resulted from methodological inconsistencies among studies, which have been extensively covered in the literature (Van Heerwaarden *et al.*, 2003; Killingbeck, 2004; Luyssaert *et al.*, 2005; Ares & Gleason, 2007). Most importantly, Van Heerwaarden *et al.* (2003) show leaf mass and leaf area loss during senescence should be accounted for in leaf P_i-resorption efficiency as these losses can underestimate resorption efficiency by 20% 10%, respectively.

Most studies involving natural soil P gradients show evidence of soil P effects on leaf P_i-resorption efficiency, at least partially. Along a strong soil P gradient in an Australian dune chronosequence, mean PRE across different species varied from zero in high-P soils to 79% in low-P soils (Hayes *et al.*, 2014). Similarly, a strong negative relationship between leaf P_i-resorption efficiency and soil P concentrations was found in the rainforests of Borneo (Hidaka & Kitayama, 2011; Tsujii *et al.*, 2017). For instance, Tsujii *et al.* (2017) found community-level mean leaf P_i-resorption efficiency varied from 24 to 93% and estimated that 20 to 37% of this variation was explained by the site, while 25 to 43% was explained by the genus, highlighting the role of adaptations in nutrient resorption. At the species level, variation in leaf P_i-resorption efficiency of a common species in neotropical forests was explained by soil P_i availability and the reproductive status of the plant, as individuals with high reproductive demands resorbed greater P amounts than those with no reproductive demands (Tully *et al.*, 2013).

Although leaf P_i-resorption efficiency has not been measured along fertility gradients in Amazonia, several small-scale studies show high variability across species and communities. In central Amazonia, mean leaf P_i-resorption efficiency among species varied from 53% to 74% (Gomes & Luizão, 2012; Machado *et al.*, 2016), in north Amazonia from 41% to 82% (Scott *et al.*, 1992; Reich *et al.*, 1995), and in northeastern Amazonia, PRE varied from 26% to 89% (Hättenschwiler *et al.*, 2011). At the community level, in a forest succession chronosequence (6 to 200 years) in eastern Amazonia, PRE varied from 53% to 73% (Reed *et al.*, 2012). Thus, leaf P_i-resorption efficiency in Amazonia is similar to the range of 24% and 93% found along the P gradient of tropical forests of Borneo (Tsujii *et al.*, 2017). We hypothesize that community-level leaf P_i-resorption efficiency in Amazonia follows the same negative relationship with soil P concentrations. Studies focused on the relationships between leaf P_i-resorption efficiency and soil P concentrations in Amazonia, following standardized methodologies, have the potential to offer valuable insights into this plant P-use strategy.

Notes S2. Effects of N on acid phosphatase exudation and activity

Root expression of phosphatases is regulated by plant P_i demand (McGill & Cole, 1981). Therefore, it is expected that as soil P_i availability decreases, C and N investments in phosphatases increase. An increase in root PME activity with N fertilization has been observed in tropical forests in Hawaii (Treseder & Vitousek, 2001) and other ecosystems (Marklein & Houlton, 2012). In contrast, N fertilization did not affect root PME activity in forests of central Amazonia (Lugli *et al.*, 2021) and Borneo (Yokoyama *et al.*, 2017), suggesting N is not a limiting factor for PME release in these forests. N and P co-limitation may happen in montane Andean forests, in the western region of Amazonia in Ecuador and Peru, where N limitation appears to increase with increasing elevation (Wullaert *et al.*, 2010; Homeier *et al.*, 2012; Fisher *et al.*, 2013), and might happen in white-sand forests (Vitousek & Sanford Jr, 1986; Martinelli *et al.*, 1999). However, currently, there is no evidence of widespread N and P co-limitation in Amazonia (Quesada *et al.*, 2010).

It has been suggested that N-fixing plants might have an advantage in P acquisition by investing excess N in the expression of phosphatases (Houlton *et al.*, 2008). In soils beneath N-fixing species, phosphatase activity was three times greater than that of other species (Houlton et al., 2008). Similarly, in tropical forests in Costa Rica and Panama and a coastal dune ecosystem in Australia, phosphatase activity was significantly greater in roots of N-fixing than non-N-fixing species (Nasto *et al.*, 2014; Png *et al.*, 2017; Batterman *et al.*, 2018). However, high root phosphatase activities in N-fixing species were most likely a result of a phylogenetically conserved strategy (Png *et al.*, 2017; Batterman *et al.*, 2018). In Amazonia, legume species are mostly facultative N-fixers and do not seem to be fixing substantial amounts of N (Vitousek *et al.*, 2002; Nardoto *et al.*, 2014). Rates of biological N fixation in a primary forest in southeastern Amazonia were about 20% of the average of other tropical forests (Wong *et al.*, 2019). This might be explained by the high N availability in most soils of Amazonia (Vitousek *et al.*, 2002; Quesada *et al.*, 2010). Alternatively, low P and low molybdenum availability could be the reason for slow rates of biological N fixation, as these might be limiting factors (Reed *et al.*, 2013; Wong *et al.*, 2019). However, increased soil P and molybdenum concentrations did not alter rates of biological N fixation in low-P soils of southeastern Amazonia (Wong *et al.*, 2019).

Currently, the few studies on root PME activity in Amazonia suggest that soil N availability is not a limiting factor in most areas. However, more studies are needed to clarify the role of soil N availability in root PME expression and the role of plant species, such as N-fixing species.

Notes S3. Cluster roots in Amazonia

Little is currently known about the formation of cluster roots in Amazonia and other tropical forests. One of the plant families most commonly cited for cluster-root formation, Proteaceae (Lambers *et al.*, 2008), has at least 13 species described in Amazonia in the Database of Brazilian plant species (REFLORA, http://floradobrasil.jbrj.gov.br/). For instance, *Roupala montana*, a widespread species in Amazonia and other neotropical forests, did not form cluster roots in soils of the Brazilian Cerrado with over 220 mg P_t kg^{-1} (mean resin-P_i varied from 5.2 to 6.6 mg kg^{-1}) but formed associations with arbuscular mycorrhizal fungi (da Silva Coutinho Detmann *et al.*, 2019). The authors suggested that soil P availability might have been high enough for these plants to still benefit from the symbiosis (da Silva Coutinho Detmann *et al.*, 2019). Although it is not typical for Proteaceae species to form associations with mycorrhizas, it has been previously observed in earlier studies (Boulet & Lambers, 2005; Lambers *et al.*, 2015). In another study, cluster roots in *R. montana* only developed in the treatment with no added P. Roots of *R. montana* were associated with significantly higher phosphatase activity and use of phytate when compared with three mycorrhizal species (Steidinger *et al.*, 2014). Although root organic acid exudation was not measured in Steidinger *et al.* (2014), the superior ability of *R. montana* to use phytate suggest that rapid rates of root organic acid exudation could have been the reason, even without the formation of cluster roots, as phytate is thought to be strongly adsorbed to the soil matrix (see Box 4; Gerke, 2015). Moreover, another species known to form cluster roots, *Euplassa cantareirae* (Proteaceae), most commonly found in the Brazilian Atlantic tropical forest, has been studied in a greenhouse experiment, and formation of its cluster roots did not depend on P supply (de Britto Costa *et al.*, 2016). More studies are necessary to find out how common the formation of cluster roots is in Amazonia and other tropical forests, under what conditions they form, and their role in P acquisition.

Table S1. Summary table of the cited studies along soil P gradients. *Mehlich-1. **Resin-P_i. ***Soil P_t concentration data.

Strategy/trait	Place	Soil P_t (mg kg^{-1})	Results	Reference
Leaf P_i resorption proficiency	Northeastern Amazonia	7 to 600	Senesced leaf P concentrations decreased with decreasing soil P_t	Soong *et al.* (2020)
	Northwestern Amazonia	40 to 480		Lips and Duivenvoorden (1996)
	Hawaii	280 to 980		Vitousek (1998); Olander and Vitousek (2000)***
	Mount Kinabalu, Borneo	20 to 417		Hidaka and Kitayama (2011)
	Mount Kinabalu, Borneo	20 to 417		Tsujii *et al.* (2017)
	Eastern China	378 to 1290		Tang *et al.* (2013)
	New Zealand	~100 to 900		Richardson *et al.* (2005); Richardson *et al.* (2004)***
	Southwestern Australia	6.6 to 432.2		Hayes *et al.* (2014)
SRL	Atlantic forest, Brazil	5.4 to 8.9*	Higher in the low-P sites	Zangaro *et al.* (2008)
	Northeastern Amazonia	3 to 36*		Metcalfe *et al.* (2008)
	New Zealand	108 to 804		Holdaway *et al.* (2011); Richardson *et al.* (2004)***
SRA	Borneo	20 to 417	Increased with declining soil P	Ushio *et al.* (2015)
	Northeastern Amazonia	3 to 36*		Metcalfe *et al.* (2008)
Fine root length	Costa Rica, Panama, Peru	200 to 1552	Increased with declining soil P	Powers *et al.* (2005)
	Hawaii	280 to 980		Ostertag (2001)
	Northwest Borneo	83 to 151		Kochsiek *et al.* (2013)
	Atlantic forest, Brazil	5.4 to 8.9*		Zangaro *et al.* (2008)
Fine root tissue density	New Zealand	108 to 804	Increased with declining soil P	Holdaway *et al.* (2011); Richardson *et al.* (2004)***
	Borneo	20 to 417	Unchanged	Ushio *et al.* (2015)
Root diameter	New Zealand	108 to 804	Declined with declining soil P	Holdaway *et al.* (2011); Richardson *et al.* (2004)***
	Atlantic forest, Brazil	5.4 to 8.9*		Zangaro *et al.* (2008)
	Borneo	20 to 417		Ushio *et al.* (2015)

Table S1. Continuation.

Strategy/trait	Place	Soil P_t (mg kg^{-1})	Results	Reference
AMF root colonization	Hawaii	280 to 980	Unchanged	Treseder and Allen (2002); Olander and Vitousek (2000)***
	Costa Rica	665 and 1601		Nasto *et al.* (2014)
	Atlantic forest	5.4 to 8.9*	Increased with declining soil P	Zangaro *et al.* (2008)
AMF Abundance in soil	Costa Rica, Panama, Peru	1552 to 600	Unchanged	Powers *et al.* (2005)
	Hawaii	280 to 980	Declined with declining soil P	Treseder and Allen (2002); Olander and Vitousek (2000)***
	Australian Dune Chronosequence	456 to 4		Teste *et al.* (2016)
	Hawaii	280 to 980		Balser *et al.* (2005)
	Northeastern Amazonia	7 to 600		Soong *et al.* (2020)
Root PME activity	Costa Rica	665 and 1601	Increased with declining soil P	Nasto *et al.* (2014)
	Borneo	20 to 417		Ushio *et al.* (2015)
	Puerto Rico	60 to 570		Cabugao *et al.* (2017); Cabugao *et al.* (2021)
	Panama	1.1 to 19.4**		Guilbeault-Mayers *et al.* (2020)
Root LMWOA exudation	Borneo	20 to 417	Increased with declining soil P	Aoki *et al.* (2012)

Table S2. Phosphorus concentrations in leaf litter in different regions of Amazonia. *Species-level measurements; unmarked references refer to community-level measurements. Although soil P concentrations were not reported in some of the studies in the north, east, and central Amazonia, these areas are considered to have very low P concentrations overall (Quesada et al., 2010). Note that these studies used different methodological approaches, e.g., litter collection timing from traps, most notably, which can affect results as litter can be rapidly decomposed.

Amazon forest region	Min ($mg\ g^{-1}$)	Max ($mg\ g^{-1}$)	Soil P_t ($mg\ kg^{-1}$)	Author
Northeast (French Guiana)	0.18 ± 0.01	0.56	10	Fanin *et al.* (2012)*
Northeast (French Guiana)	0.09	0.6	23	Hättenschwiler *et al.* (2008)*
North (Roraima, BR)	0.4	0.6	61	Scott *et al.* (1992)
Northwest (Colombia)	0.1	0.4	40 to 480	Lips and Duivenvoorden (1996)
North (Venezuela)	0.2	0.5	Not reported	Cuevas and Medina (1986)
East (Pará, BR)	0.2	0.25	Not reported	Hayashi *et al.* (2012)
East (Pará, BR)	0.41	0.75	Not reported	Dantas and Phillipson (1989)
Central (Manaus, BR)	0.2	0.6	Not reported	Klinge (1977)

Table S3. Summary table of results from P_i fertilization studies. Total soil P concentrations refer to control plots. *Soil P_t concentration data.

Indicators	Location	Soil P_t (mg kg^{-1})	Results	References
Leaf Pi-resorption proficiency	Indonesia	80 to 237	Decreased	Mirmanto *et al.* (1999)
	Hawaii	280		Vitousek (1998); Olander and Vitousek (2000)*
	Panama	600	Tended to decrease	Mayor *et al.* (2014); Wright *et al.* (2011)*
	Hawaii	980	Unchanged	Vitousek (1998); Olander and Vitousek (2000)*
	Costa Rica	1690		Alvarez-Clare and Mack (2015)
Specific root length	Central Amazonia	85	Unchanged	Lugli *et al.* (2021)
	Subtropical China	410		Liu *et al.* (2015)
	Panama	600		Wurzburger and Wright (2015); Wright *et al.* (2011)*
Fine root length	Panama	600	Tended to increase	Wurzburger and Wright (2015); Wright *et al.* (2011)*
	Hawaii	700 and 280		Ostertag (2001)
	Ecuador	450 to 525	Unchanged	Camenzind *et al.* (2016); Dietrich *et al.* (2016)*
	Subtropical China	410	Decreased	Liu *et al.* (2015)
Fine root tissue density	Central Amazonia	85	Unchanged	Lugli *et al.* (2021)
	Subtropical China	410		Liu *et al.* (2015)
	Panama	600		Wurzburger and Wright (2015); Wright *et al.* (2011)*
Diameter	Central Amazonia	85	Increased	Lugli *et al.* (2021)
	Subtropical China	410	Unchanged	Liu *et al.* (2015)
AMF root colonization	Central Amazonia	85	Unchanged	Lugli *et al.* (2021)
	Ecuador	344 ± 31		Camenzind *et al.* (2014)
	Ecuador	450 to 525		Camenzind *et al.* (2016); Dietrich *et al.* (2016)*
	Panama	600	Increased	Wurzburger and Wright (2015); Wright *et al.* (2011)*
	Hawaii	280	Tended to decrease	Treseder and Allen (2002); Olander and Vitousek (2000)*
	Subtropical China	410		Liu *et al.* (2015)
	Hawaii	980		Treseder and Allen (2002); Olander and Vitousek (2000)*

Table S3. Continuation.

Indicators	Location	Soil P_t (mg kg^{-1})	Results	References
AMF abundance in soil	Hawaii	280	Increased	Treseder and Allen (2002); Olander and Vitousek (2000)*
	Ecuador	450 to 525		Camenzind *et al.* (2016); Dietrich *et al.* (2016)*
	Panama	600	Decreased	Sheldrake *et al.* (2018); Wright *et al.* (2011)*
	Hawaii	980		Treseder and Allen (2002); Olander and Vitousek (2000)*
Root PME activity	Central Amazonia	85	Decreased	Lugli *et al.* (2021)
	Hawaii	980 to 280		Treseder and Vitousek (2001)
	Borneo	1.0 and 1.5 (Bray P)		Yokoyama *et al.* (2017)

Table S4. Root morphological traits in Amazonia, other tropical forests, and meta-analyses. Root morphological traits: specific root length (SRL, km kg^{-1}), specific root area (SRA, m^2 kg^{-1}), and root tissue density (RTD, mg cm^{-3}). N/A, not applicable (meta-analysis). *Values refer to Mehlich-1 P.

Trait	Region	Soil P_t (mg kg^{-1})	Trait variation	References
SRL	Eastern Amazon	3 to 36*	8 to 10	Metcalfe *et al.* (2008)
SRL	Central Amazon	118 to 217.4	5.9 to 41.5	Lugli *et al.* (2020)
SRL	Tropical forest in Panama	443	8 to 19.89	Wurzburger and Wright (2015)
SRL	Tropical Atlantic forest	8.9*	18.3	Zangaro *et al.* (2008)
SRL	Peruvian elevation gradient	628 to 1154	20.3 to 39.8	Girardin *et al.* (2013)
SRL	Tropical forests	N/A	7.4 to 79.3	Addo-Danso *et al.* (2020)
SRL	Tropical forests	N/A	12.2	Jackson *et al.* (1996)
SRA	Eastern Amazon	3 to 36*	24 to 34	Metcalfe *et al.* (2008)
SRA	Central Amazon	118 to 217.4	14 to 56	Lugli *et al.* (2020)
SRA	Amazon elevation gradient	628 to 1154	44 to 76	Girardin *et al.* (2013)
SRA	Tropical forests	N/A	7.9 to 87.9	Addo-Danso *et al.* (2020)
RTD	Central Amazon	118 to 217.4	141.78 to 419.22	Lugli *et al.* (2020)
RTD	Tropical forest Borneo	20 to 417	~280	Ushio *et al.* (2015)
RTD	Tropical forest Panama	443	71.8 to 328.1	Wurzburger and Wright (2015)
RTD	Tropical forests	N/A	130 to 680	Addo-Danso *et al.* (2020)

Table S5. Potential root acid phosphomonoesterase activity (PME) in Amazonia and other tropical forests. PME activity is given in µmol of substrate cleaved g^{-1} root hr^{-1}. Para-nitrophenyl phosphate (pNPP); 4-methylumbelliferyl phosphate (MUF). Note that phosphatase activity seasonally fluctuates with changes in precipitation (Turner & Wright, 2014), which may confound comparisons among one-point-in-time measurements. *Approximate mean values for N_2-fixing and non-fixing species, respectively.

Location	PME activity	Substrate	Soil P_t (mg kg^{-1})	References
Mount Kinabalu, Borneo	94 to 180	pNPP	35 to 92	Kitayama (2013)
Central Amazon	40.8	MUF	85	Lugli *et al.* (2021)
Central Amazon	36.05	MUF	148	Lugli *et al.* (2020)
Mount Kinabalu, Borneo	118 to 164	pNPP	123 to 170	Kitayama (2013)
Puerto Rico	60	pNPP	170	Cabugao *et al.* (2017)
Mount Kinabalu, Borneo	105	pNPP	274	Kitayama (2013)
Puerto Rico	36	pNPP	290	Cabugao *et al.* (2017)
Puerto Rico	25	pNPP	410	Cabugao *et al.* (2017)
Pacific, Costa Rica	~8.6 and ~6.8*	MUF	665	Nasto *et al.* (2014)
Caribbean, Costa Rica	~6.6 and ~5.3*	MUF	1601	Nasto *et al.* (2014)

Table S6. Plant and mycorrhizal responses to eCO_2 in meta-analyses; AMF (Arbuscular mycorrhizas), ECM (Ectomycorrhizas). *Mycorrhizal abundance refers to a group of indices that include percent root length/tip colonized, spore count, and extraradical hyphal length.

Mycorrhiza	Measure	eCO_2 Effect (%)	References
AMF and ECM	Mycorrhizal abundance*	+47	Treseder (2004)
AMF and ECM	Root colonization	+36	Treseder (2004)
AMF	Fungal response ratio	+21	Alberton *et al.* (2005)
ECM	Fungal response ratio	+34	Alberton *et al.* (2005)
AMF	Host-plant response ratio	+25	Alberton *et al.* (2005)
ECM	Host-plant response ratio	+26	Alberton *et al.* (2005)
AMF and ECM	Host-plant biomass	+20 ± 3	Terrer *et al.* (2016)
AMF	Host-plant biomass	+7 ± 4	Terrer *et al.* (2016)
ECM	Host-plant biomass	+30 ± 3	Terrer *et al.* (2016)
AMF and ECM	Host-plant biomass	+26	Dong *et al.* (2018)
AMF and ECM	Extraradical hyphal length	+23	Dong *et al.* (2018)
AMF and ECM	Colonization length	+15	Dong *et al.* (2018)
AMF and ECM	Fungal biomass	+22	Dong *et al.* (2018)
AMF	Fungal biomass	+7	Dong *et al.* (2018)
ECM	Fungal biomass	+30	Dong *et al.* (2018)
AMF	Host-plant biomass	+34	Dong *et al.* (2018)
ECM	Host-plant biomass	+20	Dong *et al.* (2018)
AMF	Host-plant N and P content	+22 and +19	Dong *et al.* (2018)
ECM	Host-plant N and P content	-4 and -13	Dong *et al.* (2018)

References

Addo-Danso SD, Defrenne CE, McCormack ML, Ostonen I, Addo-Danso A, Foli EG, Borden KA, Isaac ME, Prescott CE. 2020. Fine-root morphological trait variation in tropical forest ecosystems: an evidence synthesis. *Plant Ecology* **221**(1): 1-13.

Aerts R. 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* **84**(4): 597-608.

Aerts R, Chapin III FS 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*: Elsevier, 1-67.

Alberton O, Kuyper TW, Gorissen A. 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO_2. *New Phytologist* **167**(3): 859-868.

Alvarez-Clare S, Mack MC. 2015. Do foliar, litter, and root nitrogen and phosphorus concentrations reflect nutrient limitation in a lowland tropical wet forest? *PloS one* **10**(4): e0123796.

Aoki M, Fujii K, Kitayama K. 2012. Environmental control of root exudation of low-molecular weight organic acids in tropical rainforests. *Ecosystems* **15**(7): 1194-1203.

Ares A, Gleason SM 2007. Foliar nutrient resorption in tree species. *New Research on Forest Ecology*, 1-32.

Balser T, Treseder K, Ekenler M. 2005. Using lipid analysis and hyphal length to quantify AM and saprotrophic fungal abundance along a soil chronosequence. *Soil Biology and Biochemistry* **37**(3): 601-604.

Batterman SA, Hall JS, Turner BL, Hedin LO, LaHaela Walter JK, Sheldon P, van Breugel M. 2018. Phosphatase activity and nitrogen fixation reflect species differences, not nutrient trading or nutrient balance, across tropical rainforest trees. *Ecology Letters* **21**(10): 1486-1495.

Boulet FM, Lambers H. 2005. Characterisation of arbuscular mycorrhizal fungi colonisation in cluster roots of shape *Hakea verrucosa* F. Muell (Proteaceae), and its effect on growth and nutrient acquisition in ultramafic soil. *Plant and Soil* **269**(1): 357-367.

Cabugao KG, Timm CM, Carrell AA, Childs J, Lu T-YS, Pelletier DA, Weston DJ, Norby RJ. 2017. Root and rhizosphere bacterial phosphatase activity varies with tree species and soil phosphorus availability in Puerto Rico tropical forest. *Frontiers in plant science* **8**: 1834.

Cabugao KG, Yaffar D, Stenson N, Childs J, Phillips J, Mayes MA, Yang X, Weston DJ, Norby RJ. 2021. Bringing function to structure: Root–soil interactions shaping phosphatase activity throughout a soil profile in Puerto Rico. *Ecology and evolution* **11**(3): 1150-1164.

Camenzind T, Hempel S, Homeier J, Horn S, Velescu A, Wilcke W, Rillig MC. 2014. Nitrogen and phosphorus additions impact arbuscular mycorrhizal abundance and molecular diversity in a tropical montane forest. *Global Change Biology* **20**(12): 3646-3659.

Camenzind T, Homeier J, Dietrich K, Hempel S, Hertel D, Krohn A, Leuschner C, Oelmann Y, Olsson PA, Suárez JP. 2016. Opposing effects of nitrogen versus phosphorus additions on mycorrhizal fungal abundance along an elevational gradient in tropical montane forests. *Soil Biology and Biochemistry* **94**: 37-47.

Cuevas E, Medina E. 1986. Nutrient dynamics within Amazonian forest ecosystems. *Oecologia* **68**(3): 466-472.

da Silva Coutinho Detmann K, de Souza Leite T, de Oliveira Neto RR, Delgado MN, Rebello VPA, Azevedo AA, Kasuya MCM, Selosse M-A, de Almeida AM. 2019. Arbuscular mycorrhizae and absence of cluster roots in the Brazilian Proteaceae *Roupala montana* Aubl. *Symbiosis* **77**(2): 115-122.

Dantas M, Phillipson J. 1989. Litterfall and litter nutrient content in primary and secondary Amazonian 'terra firme' rain forest. *Journal of Tropical Ecology* **5**(1): 27-36.

de Britto Costa P, Abrahão A, Viani RAG, Brancalion PHS, Lambers H, Sawaya ACHF, Oliveira RS. 2016. Cluster-root formation and carboxylate release in *Euplassa cantareirae* (Proteaceae) from a neotropical biodiversity hotspot. *Plant and Soil* **403**(1-2): 267-275.

Dietrich K, Spoeri E, Oelmann Y. 2016. Nutrient addition modifies phosphatase activities along an altitudinal gradient in a tropical montane forest in Southern Ecuador. *Frontiers in Earth Science* **4**: 12.

Dong Y, Wang Z, Sun H, Yang W, Xu H. 2018. The response patterns of arbuscular mycorrhizal and ectomycorrhizal symbionts under elevated CO_2: a meta-analysis. *Frontiers in microbiology* **9**: 1248.

Eckstein RL, Karlsson P, Weih M. 1999. Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytologist* **143**(1): 177-189.

Fanin N, Barantal S, Fromin N, Schimann H, Schevin P, Hättenschwiler S. 2012. Distinct microbial limitations in litter and underlying soil revealed by carbon and nutrient fertilization in a tropical rainforest. *PloS one* **7**(12): e49990.

Fisher JB, Malhi Y, Torres IC, Metcalfe DB, van de Weg MJ, Meir P, Silva-Espejo JE, Huasco WH. 2013. Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia* **172**(3): 889-902.

Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, Fuchslueger L, Garcia S, Goll DS, Grandis A, Jiang M. 2019. Amazon forest response to CO_2 fertilization dependent on plant phosphorus acquisition. *Nature Geoscience* **12**(9): 736-741.

Gerke J. 2015. Phytate (inositol hexakisphosphate) in soil and phosphate acquisition from inositol phosphates by higher plants. A review. *Plants* **4**(2): 253-266.

Girardin C, Aragão L, Malhi Y, Huaraca Huasco W, Metcalfe D, Durand L, Mamani M, Silva-Espejo J, Whittaker R. 2013. Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles* **27**(1): 252-264.

Gomes AC, Luizão FJ. 2012. Leaf and soil nutrients in a chronosequence of second-growth forest in central Amazonia: implications for restoration of abandoned lands. *Restoration Ecology* **20**(3): 339-345.

Guilbeault-Mayers X, Turner BL, Laliberté E. 2020. Greater root phosphatase activity of tropical trees at low phosphorus despite strong variation among species. *Ecology* **101**(8): e03090. doi: 10.1002/ecy.3090

Han W, Tang L, Chen Y, Fang J. 2013. Relationship between the relative limitation and resorption efficiency of nitrogen vs phosphorus in woody plants. *PloS one* **8**(12): e83366.

Hättenschwiler S, Aeschlimann B, Coûteaux MM, Roy J, Bonal D. 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. *New Phytologist* **179**(1): 165-175.

Hättenschwiler S, Coq S, Barantal S, Handa IT. 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *New Phytologist* **189**(4): 950-965.

Hayashi SN, Vieira ICG, Carvalho CJR, Davidson E. 2012. Linking nitrogen and phosphorus dynamics in litter production and decomposition during secondary forest succession in the eastern Amazon. *Embrapa Amazônia Oriental-Artigo em periódico indexado (ALICE)*.

Hayes P, Turner BL, Lambers H, Laliberté E. 2014. Foliar nutrient concentrations and resorption efficiency in plants of contrasting nutrient-acquisition strategies along a 2-million-year dune chronosequence. *Journal of Ecology* **102**(2): 396-410.

He M, Yan Z, Cui X, Gong Y, Li K, Han W. 2020. Scaling the leaf nutrient resorption efficiency: Nitrogen vs phosphorus in global plants. *Science of The Total Environment*: 138920.

Hidaka A, Kitayama K. 2011. Allocation of foliar phosphorus fractions and leaf traits of tropical tree species in response to decreased soil phosphorus availability on Mount Kinabalu, Borneo. *Journal of Ecology* **99**(3): 849-857.

Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. 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.

Homeier J, Hertel D, Camenzind T, Cumbicus NL, Maraun M, Martinson GO, Poma LN, Rillig MC, Sandmann D, Scheu S. 2012. Tropical Andean forests are highly susceptible to nutrient inputs—Rapid effects of experimental N and P addition to an Ecuadorian montane forest. *PloS one* **7**(10): e47128.

Houlton BZ, Wang Y-P, Vitousek PM, Field CB. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* **454**(7202): 327-330.

Jackson R, Canadell J, Ehleringer JR, Mooney H, Sala O, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**(3): 389-411.

Killingbeck KT 2004. Nutrient resorption. In: Noodén LD ed. *Plant Cell Death Processes*. San Diego: Academic Press, 215-226.

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): 215-224.

Klinge H. 1977. Preliminary data on nutrient release from decomposing leaf litter in a neotropical rain forest. *Amazoniana: Limnologia et Oecologia Regionalis Systematis Fluminis Amazonas* **6**(2): 193-202.

Kochsiek A, Tan S, Russo SE. 2013. Fine root dynamics in relation to nutrients in oligotrophic Bornean rain forest soils. *Plant Ecology* **214**(6): 869-882.

Lambers H, Clode PL, Hawkins H-J, Laliberté E, Oliveira RS, Reddell P, Shane MW, Stitt M, Weston P 2015. Metabolic Adaptations of the Non-Mycotrophic Proteaceae to Soils With Low Phosphorus Availability. *Annual Plant Reviews Volume 48*, 289-335.

Lambers H, Raven JA, Shaver GR, Smith SE. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends in Ecology & Evolution* **23**(2): 95-103.

Lips JM, Duivenvoorden JF. 1996. Fine litter input to terrestrial humus forms in Colombian Amazonia. *Oecologia* **108**(1): 138-150.

Liu B, Li H, Zhu B, Koide RT, Eissenstat DM, Guo D. 2015. Complementarity in nutrient foraging strategies of absorptive fine roots and arbuscular mycorrhizal fungi across 14 coexisting subtropical tree species. *New Phytologist* **208**(1): 125-136.

Lugli LF, Andersen KM, Aragão LE, Cordeiro AL, Cunha HF, Fuchslueger L, Meir P, Mercado LM, Oblitas E, Quesada CA. 2020. Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil* **450**: 49-63.

Lugli LF, Rosa JS, Andersen KM, Di Ponzio R, Almeida RV, Pires M, Cordeiro AL, Cunha HF, Martins NP, Assis RL. 2021. Rapid responses of root traits and productivity to phosphorus and cation additions in a tropical lowland forest in Amazonia. *New Phytologist* **230**(1): 116-128.

Luyssaert S, Staelens J, De Schrijver A. 2005. Does the commonly used estimator of nutrient resorption in tree foliage actually measure what it claims to? *Oecologia* **144**(2): 177-186.

Machado MR, Sampaio PdTB, Ferraz J, Camara R, Pereira MG. 2016. Nutrient retranslocation in forest species in the Brazilian Amazon. *Acta Scientiarum. Agronomy* **38**(1): 93-101.

Marklein AR, Houlton BZ. 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. *New Phytologist* **193**(3): 696-704.

Martinelli L, Piccolo M, Townsend A, Vitousek P, Cuevas E, McDowell W, Robertson G, Santos O, Treseder K. 1999. Nitrogen stable isotopic composition of leaves and soil: tropical versus temperate forests. *Biogeochemistry* **46**(1): 45-65.

Mayor JR, Wright SJ, Turner BL. 2014. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. *Journal of Ecology* **102**(1): 36-44.

McGill W, Cole C. 1981. Comparative aspects of cycling of organic C, N, S and P through soil organic matter. *Geoderma* **26**(4): 267-286.

Metcalfe DB, Meir P, Aragão LEO, da Costa AC, Braga AP, Gonçalves PH, Junior JdAS, de Almeida SS, Dawson LA, Malhi Y. 2008. The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil* **311**(1-2): 189-199.

Mirmanto E, Proctor J, Green J, Nagy L, Suriantata. 1999. Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **354**(1391): 1825-1829.

Nardoto GB, Quesada CA, Patiño S, Saiz G, Baker TR, Schwarz M, Schrodt F, Feldpausch TR, Domingues TF, Marimon BS. 2014. Basin-wide variations in Amazon forest nitrogen-cycling characteristics as inferred from plant and soil 15N: 14N measurements. *Plant Ecology & Diversity* **7**(1-2): 173-187.

Nasto MK, Alvarez-Clare S, Lekberg Y, Sullivan BW, Townsend AR, Cleveland CC. 2014. Interactions among nitrogen fixation and soil phosphorus acquisition strategies in lowland tropical rain forests. *Ecology Letters* **17**(10): 1282-1289.

Olander LP, Vitousek PM. 2000. Regulation of soil phosphatase and chitinase activityby N and P availability. *Biogeochemistry* **49**(2): 175-191.

Ostertag R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* **82**(2): 485-499.

Png GK, Turner BL, Albornoz FE, Hayes PE, Lambers H, Laliberté E. 2017. Greater root phosphatase activity in nitrogen-fixing rhizobial but not actinorhizal plants with declining phosphorus availability. *Journal of Ecology* **105**(5): 1246-1255.

Powers JS, Treseder KK, Lerdau MT. 2005. Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances. *New Phytologist* **165**(3): 913-921.

Quesada C, Lloyd J, Schwarz M, Patino S, Baker T, Czimczik C, Fyllas N, Martinelli L, Nardoto G, Schmerler J. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* **7**(5): 1515-1541.

Reed SC, Cleveland CC, Townsend AR. 2013. Relationships among phosphorus, molybdenum and free-living nitrogen fixation in tropical rain forests: results from observational and experimental analyses. *Biogeochemistry* **114**(1): 135-147.

Reed SC, Townsend AR, Davidson EA, Cleveland CC. 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. *New Phytologist* **196**(1): 173-180.

Reich PB, Ellsworth D, Uhl C. 1995. Leaf carbon and nutrient assimilation and conservation in species of differing successional status in an oligotrophic Amazonian forest. *Functional Ecology*: 65-76.

Richardson SJ, Peltzer DA, Allen RB, McGlone MS. 2005. Resorption proficiency along a chronosequence: responses among communities and within species. *Ecology* **86**(1): 20-25.

Richardson SJ, Peltzer DA, Allen RB, McGlone MS, Parfitt RL. 2004. Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. *Oecologia* **139**(2): 267-276.

Scott D, Proctor J, Thompson J. 1992. Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil. II. Litter and nutrient cycling. *Journal of Ecology*: 705-717.

Sheldrake M, Rosenstock NP, Mangan S, Revillini D, Sayer EJ, Olsson PA, Verbruggen E, Tanner EV, Turner BL, Wright SJ. 2018. Responses of arbuscular mycorrhizal fungi to long-term inorganic and organic nutrient addition in a lowland tropical forest. *The ISME journal* **12**(10): 2433-2445.

Soong JL, Janssens IA, Grau O, Margalef O, Stahl C, Van Langenhove L, Urbina I, Chave J, Dourdain A, Ferry B. 2020. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. *Scientific Reports* **10**(1): 1-13.

Steidinger BS, Turner BL, Corrales A, Dalling JW. 2014. Variability in potential to exploit different soil organic phosphorus compounds among tropical montane tree species. *Functional Ecology* **29**(1): 121-130.

Tang L, Han W, Chen Y, Fang J. 2013. Resorption proficiency and efficiency of leaf nutrients in woody plants in eastern China. *Journal of Plant Ecology* **6**(5): 408-417.

Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC. 2016. Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* **353**(6294): 72-74.

Teste FP, Laliberté E, Lambers H, Auer Y, Kramer S, Kandeler E. 2016. Mycorrhizal fungal biomass and scavenging declines in phosphorus-impoverished soils during ecosystem retrogression. *Soil Biology and Biochemistry* **92**: 119-132.

Treseder KK. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytologist* **164**(2): 347-355.

Treseder KK, Allen MF. 2002. Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. *New Phytologist* **155**(3): 507-515.

Treseder KK, Vitousek PM. 2001. Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology* **82**(4): 946-954.

Tsujii Y, Onoda Y, Kitayama K. 2017. Phosphorus and nitrogen resorption from different chemical fractions in senescing leaves of tropical tree species on Mount Kinabalu, Borneo. *Oecologia* **185**(2): 171-180.

Tully KL, Wood TE, Schwantes AM, Lawrence D. 2013. Soil nutrient availability and reproductive effort drive patterns in nutrient resorption in *Pentaclethra macroloba*. *Ecology* **94**(4): 930-940.

Turner BL, Wright SJ. 2014. The response of microbial biomass and hydrolytic enzymes to a decade of nitrogen, phosphorus, and potassium addition in a lowland tropical rain forest. *Biogeochemistry* **117**(1): 115-130.

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.

Van Heerwaarden L, Toet S, Aerts R. 2003. Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos* **101**(3): 664-669.

Vitousek PM. 1998. Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. *Ecosystems* **1**(4): 401-407.

Vitousek PM, Cassman K, Cleveland C, Crews T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB 2002. Towards an ecological understanding of biological nitrogen fixation. *The Nitrogen Cycle at Regional to Global Scales*: Springer, 1-45.

Vitousek PM, Sanford Jr RL. 1986. Nutrient cycling in moist tropical forest. *Annual review of ecology and systematics* **17**(1): 137-167.

Wang Z, Fan Z, Zhao Q, Wang M, Ran J, Huang H, Niklas KJ. 2018. Global data analysis shows that soil nutrient levels dominate foliar nutrient resorption efficiency in herbaceous species. *Frontiers in plant science* **9**: 1431.

Wong MY, Neill C, Marino R, Silvério DV, Brando PM, Howarth RW. 2019. Biological nitrogen fixation does not replace nitrogen losses after forest fires in the southeastern Amazon. *Ecosystems*: 1-19.

Wright IJ, Westoby M. 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. *Functional Ecology* **17**(1): 10-19.

Wright SJ, Yavitt JB, Wurzburger N, Turner BL, Tanner EV, Sayer EJ, Santiago LS, Kaspari M, Hedin LO, Harms KE. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* **92**(8): 1616-1625.

Wullaert H, Homeier J, Valarezo C, Wilcke W. 2010. Response of the N and P cycles of an old-growth montane forest in Ecuador to experimental low-level N and P amendments. *Forest Ecology and Management* **260**(9): 1434-1445.

Wurzburger N, Wright SJ. 2015. Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology* **96**(8): 2137-2146.

Yokoyama D, Imai N, Kitayama K. 2017. Effects of nitrogen and phosphorus fertilization on the activities of four different classes of fine-root and soil phosphatases in Bornean tropical rain forests. *Plant and Soil* **416**(1-2): 463-476.

Yuan Z, Chen HY. 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. *Global Ecology and Biogeography* **18**(1): 11-18.

Zangaro W, de Assis RL, Rostirola LV, de Souza PB, Gonçalves MC, Andrade G, Nogueira MA. 2008. Changes in arbuscular mycorrhizal associations and fine root traits in sites under different plant successional phases in southern Brazil. *Mycorrhiza* **19**(1): 37-45.