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Title: **Stocks and biogeochemical cycling of soil-derived nutrients in an ultramafic rain forest in New Caledonia**

Running Title: **Nutrient Cycling in an ultramafic forest**

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CONFLICTS OF INTEREST/COMPETING INTERESTS

The authors declare no conflict of interest.

ABSTRACT

Ultramafic rain forests in New Caledonia evolved on some of the most nutrient impoverished soils globally and are some of the slowest-growing tropical forests known. This study aimed to determine nutrient stocks and elucidate the biogeochemical cycling of nutrients in a remnant lowland rain forest in southern New Caledonia. Based on an inventory of a 1-ha permanent plot, exhaustive plant tissue sampling was undertaken of all large trees (diameter at breast height ≥15 cm) in a 0.25-ha subset of the plot in concert with 100 soil samples. All samples were analyzed for major nutrient concentrations and the results show that most of the magnesium was contained in the soil (96.9%), whereas a large fraction of calcium (46.5%) and phosphorus (16.0%), and the majority the potassium (81.5%) were contained in the standing biomass. This study has shown how tightly these soil-derived nutrients are cycling in this system. Ultimately, this information will be essential for efforts to restore rain forest in New Caledonia, where the biomass (and contained nutrients) has been removed.

KEYWORDS

Environmental restoration, New Caledonia, Nutrient Cycling, Potassium, Radiocarbon dating, Rain Forest, Ultramafic.

INTRODUCTION

The biogeochemical cycling of nutrients comprises a broad array of direct and indirect interactions and processes (*e.g.* nutrient uptake and storage, litter production and decomposition) involving microbiome, plant, and abiotic factors such as topography and climate (Hobbie 1992, Foster and Bhatti 2006, Bahram et al. 2018). The complexity of deciphering rain forest nutrient cycling lies in estimating the quantities of nutrients in the various pools and the prevalence of the interconnecting flows (Proctor 1987). These processes occur at different time scales, and ecosystem stability relies on their synchrony, as disturbance of one process, if not compensated, may start a chain reaction causing asynchrony (Myers et al. 1994). Simplified nutrient cycling conceptual models use two arbitrary categories, 'short' and 'long', to describe the processes responsible for mineral turnover in ecosystems (Proctor 1987). Short cycling includes small litterfall and immediate processes occurring during and after rainfall (*e.g.,* stemflow, throughflow). In contrast, long cycling includes tree biomass growth, weathering, leaching, and other soil processes that concomitantly and continuously occur over extended periods (Proctor 1987).

Nutrients in forests need to be supplied *via* ecosystem enrichment processes and internally recycled to satisfy growth requirements (Wanek et al. 2008). Generally, nutrients escape from ecosystems *via* soil leaching and erosion after incorporation through weathering or atmospheric deposition onto ecosystems that have developed on weathered soils (Chadwick et al. 1999). The nutrient limitations observed in many terrestrial ecosystems (especially nitrogen – N – and phosphorus – P) result from the concomitant occurrence of numerous constraining mechanisms. In the case of P, the primary mechanism leading to the widespread occurrence of nutrient-limited ecosystems is the low concentration found in parent materials (Vitousek 1984, Vitousek and Sanford 1986). Furthermore, a high content of iron (Fe)-oxides naturally occludes P and significantly limits its availability (Vitousek et al. 2010). In New Caledonia, this is especially true for substrates derived from ultramafic rocks that are naturally rich in Fe-oxides (Schwertmann and Latham 1986, Quantin et al. 1997). The storage and partitioning of nutrients in rain forest ecosystems are diverse and complex as they occur over a broad range of substrates (Proctor 1987). For example, a study in New South Wales, Australia, comparing ‘rich’ and ‘poor’ soils showed that specific nutrient utilization varied significantly between localities with lower nutrient availability synonymous with higher nutrient use efficiency (Lambert et al. 2016). Nonetheless, little is known about rain forest nutrient flows and nutrient budgets in ultramafic areas because of the complexity and the wide range of mechanisms involved (*e.g.* bedrock weathering, microbial activity) despite the reporting of more and more sophisticated studies (*e.g.* Johnson et al. 2001, Fujii et al. 2011, Nasto et al. 2017).

The ‘biogeochemical niche’ hypothesis suggests that multiple plant species thrive in the same ecosystem as a result of a balance in nutrient uses obtained through time to limit competition (*e.g.* growth, uptake, soil space – Garten 1978, Peñuelas et al. 2010, 2019, Urbina et al. 2017). According to Ågren and Weih (2012), plant nutrient concentration differences within ecosystems mainly result from the soil elemental availability diversities. The co-occurrence of these factors, especially in slow-growing plant communities, ultimately leads to extremely complex and diverse plant assemblages. It also possibly explains the high elemental concentrations found in certain species compared to the substrate on which they are growing (van Breemen 1995, Fyllas and Troumbis 2009). Slow-growing species are *de facto* adapted by their low nutrient needs, efficient recycling, and uptake mechanisms to nutrient-limited ecosystems (Chapin 1980).

Ultramafic soils which develop from the weathering of ultramafic rocks cover ~3% of the Earth's surface. Most ultramafic substrates are highly infertile, but ultramafic substrates and especially Ferralsols are among the most constraining soils for plant growth due to the lack of clay minerals, acidic pH, low CEC, major nutrient deficiencies, and high cobalt (Co), chromium (Cr), manganese (Mn) and nickel (Ni) concentrations (van der Ent et al. 2015, Pillon et al. 2020, Echevarria 2021). One of the largest ultramafic terranes (~5500 km^2) occurs in New Caledonia – an archipelago ~1500 km east of Australia in the southern tropical zone north of the Tropic of Capricorn (Maurizot et al. 2020). It is renowned for its exceptional biodiversity with ~3300 vascular plant species, of which ~2100 grow on ultramafic substrates including over 180 metal hyperaccumulator species (Isnard et al. 2016; Gei et al. 2020).

These plants that may accumulate more than 100 times more of a metal than most other metallophytes and represent one of the best examples of plant adaptation to harsh environments (van der Ent et al. 2013). Two highly discernible vegetation types occur on New Caledonian ultramafic soils: various types of rain forests and the maquis (Jaffré 1980). The presence of some families (*e.g.* Myrtaceae, Rubiaceae) or conifers (Gymnosperms) on ultramafic soils results from the occurrence of specific physiological attributes, which include low foliar P and potassium (K) or the ability to cope with an imbalanced calcium (Ca)/magnesium (Mg) quotient or high concentrations of Ni and Mn in the soil (Jaffré 1980).

The current study aimed to determine the biogeochemical cycling of nutrients and to establish to what degree these nutrients are 'locked up' in living biomass in a New Caledonian ultramafic forest. To that end, exhaustive sampling was undertaken to calculate the amounts of N, P, K, Ca, and Mg in both standing biomass and soil, as well as the topsoil enrichment and the returns from litterfall. Ultimately, this information will help restore rain forests in New Caledonia where clear-felling has taken place.

MATERIALS AND METHODS

Location and condition of the plot and census of tree flora

The study plot (22° 16′29″ S, 166° 54′14″ E; ~270 to ~300 a.s.l) was in the Grand Massif du Sud, one of the world's largest ultramafic massifs which dominates the southern part of Grande Terre in New Caledonia (Figure S1). The local rain forest established over harzburgite bedrock (Table S1) that weathered into a Geric Ferralsol (Becquer et al., 2001). The area is in a tropical oceanic zone with an annual rainfall of ~3300 mm. The climate of New Caledonia is divided into 'hot' and 'cool' seasons (Météo France 2020). The hot season (>300 mm precipitation month^{-1} and mean temperature >28 ºC) lasts from January to April and the cool season (<250 mm precipitation month^{-1} and mean temperature <25 ºC) continues from June to September while transition periods occur in May and later from October to December (Météo France 2020). Plot data were obtained from the rain forest plot network NC-PIPPN established across New Caledonia (Ibanez et al. 2013, Birnbaum et al. 2015). The current study was undertaken in a 0.25-ha subplot located in the center of a 1-ha plot (Figure 1). The 0.25-ha plot was subdivided into 100 subplots (5 m × 5 m).

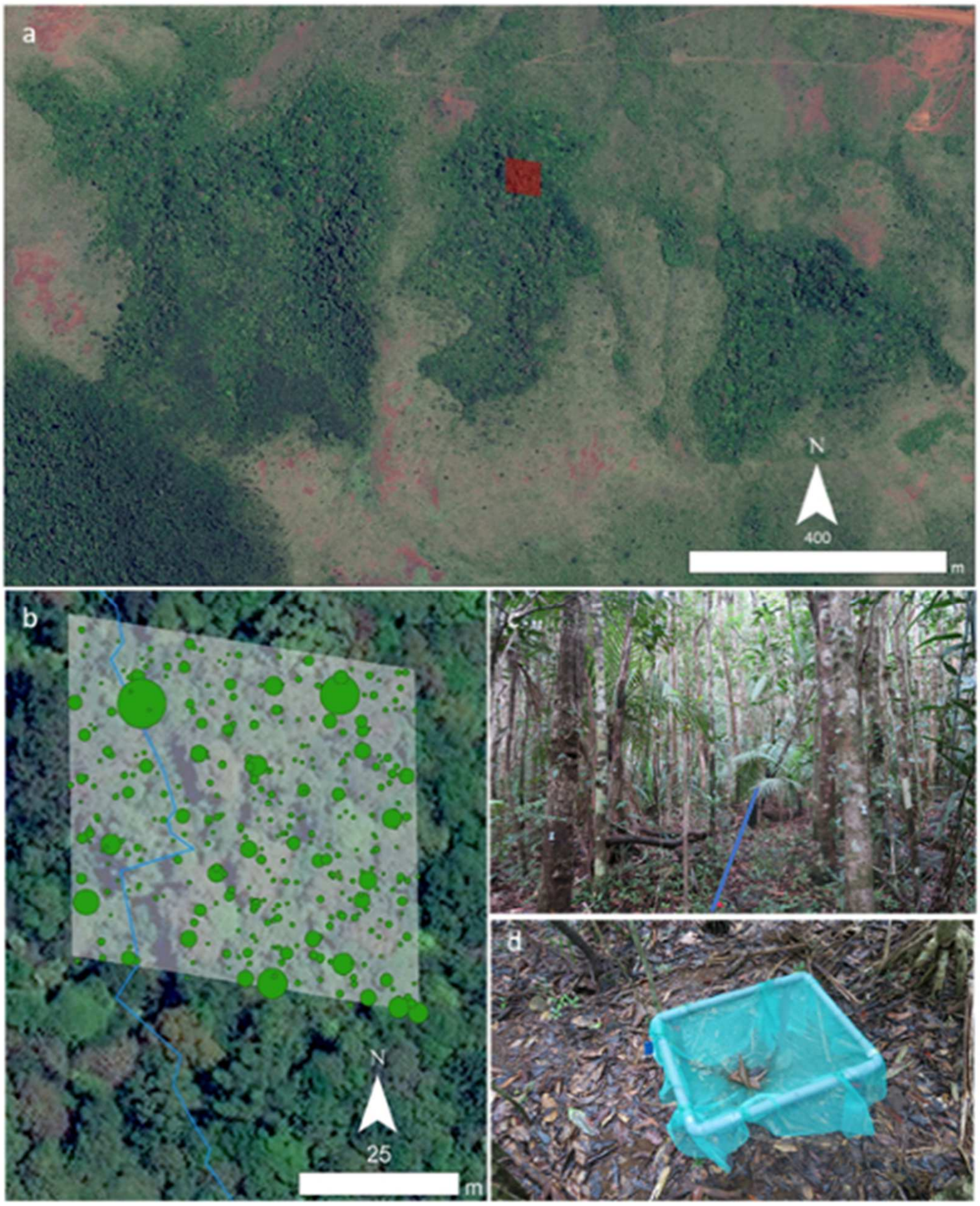

Figure 1. Location of the plot and trees in the Plaine de Lac (New Caledonia) and collection protocol. a: Remnant primary lowland rain forest surrounding the plot. b: Close-up image of the plot with all the trees overlaying. Worldview-3 imagery. The size of the filled circles indicates the individual tree diameters, and the blue line indicates the position of the creek. c: Picture of the plot on the first day of collection as the plot was delineated with cords (highlighted in blue). d: Picture of one of the twelve 0.25 m^2 litterfall traps.

Collection of plant and soil samples

One or two branches (~2 cm diameter) accessible with a long-reach tree pruner (20 m long) were cut off from all trees with a dbh (diameter at breast height) >15 cm and Ni hyperaccumulators with a dbh >10 cm for chemical analysis. Old leaves (first four leaves), young leaves (last four leaves), twigs (last few centimeters), wood/branch (first few centimeters), and the xylem sap (using a vacuum pump – Alexou and Peuke 2013) were collected from each branch (Paul et al. 2021). Twelve litterfall traps (0.25 m^2) were set up randomly to collect the litterfall monthly over 12 months (Figure 1d). Soil samples were collected at four different depths in each subplot (0–5 cm, 5–10 cm, 10–15 cm, and 15–20 cm) using a soil core sampler (5 cm diameter).

Processing of collected samples

Solid plant samples were oven-dried at 60 °C for 72 h, wood and bark were separated using a sharp box cutter and the bulk litterfall was weighted. All plant materials were subsequently ground to a fine powder using an impact mill, thoroughly homogenized, and weighed to create ~300 mg samples. Xylem sap and latex samples were freeze-dried (-85 °C at <0.003 mbar) for two days. All plant samples were then pre-digested with 7 mL HNO_3 (70%) for 48 h before being digested in a microwave oven (Milestone Start D) at 125 °C for 45 min. Soil samples were air-dried for five days and subsequently sieved through 2 mm screens. Soil pH was measured in a 1:2.5 soil:water slurry after 1-hour equilibration time. Sub-samples (~300 mg) were digested with 2 mL HCl (37%) and 5 mL HNO_3 (70%) in a ColdBlock system at 50% power (CB15S 15 channel system, ColdBlock Technologies Inc) to determine pseudo-total trace element concentrations (Wang et al. 2013). The cation exchange capacity (CEC) and exchangeable cations of the soil (Ca_{ex}, K_{ex}, and Mg_{ex}) were determined by weighing 800 mg of each of the samples into 50 mL tubes to which 40 mL of unbuffered silver thiourea

(0.01 *M* Ag^+) was added. Tubes were then shaken overnight (16–20 h) in the dark and subsequently centrifuged to collect the clear supernatant liquid (Dohrmann 2006). All samples were diluted if needed using ultrapure water (Millipore 18.2 MΩ cm at 25 °C) before analysis *via* Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES; Thermo Scientific iCAP 7400 instrument) in radial mode for Ca, K, Mg and P (Material S1). Soils (top 5 cm only), young leaves and litterfall nitrogen was analyzed using a Vario ELcube (Elementar Analysensysteme GmbH).

^{14}C analysis of a large Pycnandra acuminata tree

The age of a large individual of *Pycnandra acuminata* (Sapotaceae) was determined to obtain insight into the age of the forest stand. The sampled core for ^{14}C dating was collected in March 2019 using a Haglöf increment borer from one large *P. acuminata* (dbh ~35 cm). The sample was sent to the NEIF Radiocarbon Laboratory for pre-treatment (Material S2) and subsequently on to the Scottish Universities Environmental Research Centre AMS Laboratory for ^{14}C dating using an NEC accelerator mass spectrometer.

Statistical analyses

Statistical analyses were done using version 1.2.5042 of the Rstudio software (PBC). The Waller-Duncan K-ratio t-test was used when data were both normal and homoscedastic. If one of the assumptions was violated, data were transformed to meet both assumptions. A α level of 0.05 was used to define statistical significance for each test. Near neighbor interpolations were carried out with ArcMap software (ESRI), version 10.7.1 (2019-06-27) to create the elemental maps. For all families, the family importance value (FIV) was calculated based on the formula developed by Mori et al. (1983). Additionally, the importance value index (IVI) was used to demonstrate the importance of a species in the plot and was defined as the sum of relative frequency, relative dominance, and relative density (Misra 1968). Total plant biomass was calculated *via* the 7th model proposed by Chave et al. (2014), while plant part masses (*i.e.* leaves, branches, stems) were estimated using ratios determined from the tropical rain forest allometric formula proposed by Yamakura et al. (1986). Wood densities were obtained from external organization databases from the literature (*e.g.* ICRAF Database 2019) or in the NC-PIPPN database (Birnbaum et al. 2015). In the absence of value for a species, wood density was extrapolated from the values known for the genus (Chave et al. 2006). Nutrient stocks in biomass were obtained by multiplying tree plant part biomass by the corresponding plant part concentration. Nitrogen concentrations in wood were calculated using the equation: wood N = (0.33 x leaf N) - 0.15 developed from Malaysian tropical forest trees (F. Q. Brearley, unpublished). Nutrient stocks in the soil were obtained by multiplying the concentration in each layer (top 20 cm) by the soil's estimated mass in that layer.

RESULTS

Forest floristic diversity and physiognomy of the plot

The 0.25-ha plot had 349 trees in total (189 trees over 15 cm dbh) belonging to 35 families, 52 genera, and 64 species, corresponding to a Fisher's alpha of 23.0. Only two families (Myrtaceae and Sapotaceae) had more than three species in the plot with 10 and 6 species, respectively. The Myrtaceae and Sapotaceae also had the highest FIV (42.7 and 36.3), making them the most important families in the plot (Table S2). Seven other families had a FIV >10, with the Sapindaceae (25.8) and Bignoniaceae (15.6) having the largest values while the first nine families accounted for >60% of the overall FIV (Result S1). *Storthocalyx chryseus* (Sapindaceae), *Deplanchea speciosa* (Bignoniaceae), and *P. acuminata* were the three most important species according to the IVI and the most abundant in the plot along with

Sparattosyce dioica (Moraceae), and *Cunonia balansae* (Cunoniaceae) (Table S3 and Result S1).

	Ca	**K**	**Mg**	**P**	**P**
Young leaves	5690 d (513–26 400)	8390 a (1250–36 900)	2690 a (792–9380)	9.50 (4.60–26.4)	347 a (127–1800)
Old leaves	7510 c (557–36 200)	4570 b (1140–16 600)	2660 a (609–9280)	–	245 b (111–825)
Twigs	13 300 a (1420–65 600)	7470 a (206–32 300)	2640 a (457–12 300)	–	329 a (74.0–1740)
Bark	9860 b (796–57 400)	4050 c (501–13 100)	1140 b (378–6250)	–	133 c (34.6–772)
Wood	2540 e (346–21 000)	2560 d (355–12 200)	455 c (95.8–4820)	–	84.5 d (19.3–713)
Xylem sap	42.7 f (4.86–464)	108 f (1.19–506)	20.8 f (1.03–121)	1.82 f (<LoD–36.1)	

Table 1. Concentration of Ca, K, Mg and P in plant tissue parts in the Plaine de Lac (New Caledonia). Concentrations (mg kg^{-1}) are summarized as median (minimum-maximum). *Footnote: Medians followed by the same letter are not significantly different at the 5% level according to the Waller-Duncan means separation test.*

Concentrations of major nutrients in trees of the plot

Median Ca concentrations varied from 2540 mg Ca kg^{-1} to 13 300 mg Ca kg^{-1} across all tissues, being greatest in twigs and was ~42.7 mg kg^{-1} in xylem sap (Table 1). Of the FIV top 10, the Clusiaceae and Cunoniaceae had the highest Ca concentrations (twigs over 18 000 mg kg^{-1}) while Sapindaceae (S. chryseus) had the lowest concentrations (<2000 mg kg^{-1} in twigs) in the plot (Table S4). Young leaves and twigs were significantly enriched in K (>7000 mg kg^{-1}) compared to other plant parts (Table 1), while Moraceae, Bignoniaceae and Sapindaceae presented, on average, the highest median K concentrations within the prominent families (Table S5). The median Mg concentrations ranged from 455 mg to 2690 mg kg^{-1} with significantly higher concentrations in the twigs, young leaves, and old leaves (Table 1). Among the main families in the plot, Moraceae had the highest Mg concentrations up to 12 300 mg Mg kg^{-1} in twigs (Table S6). No significant differences in foliar N concentrations were observed across families nor species (Table S7) with concentrations ranging from 4.8 mg to 26.4 mg N g^{-1}. Median P concentrations varied from 84.5 mg to 347 mg P kg^{-1} in tissues with higher concentrations in young leaves and twigs (> 320 mg P kg^{-1}) while xylem sap concentrations were below the limits of detection (ICP reading below 0.10 mg L^{-1}) for most species (Table 1). Among the main families, Sapindaceae had significantly higher P concentrations than others (Table S7). Calcium was the only element that was found to be strongly and negatively correlated with both IVI and FIV ($p < 0.001$), while no trends could be observed for the other elements.

Soil chemistry of the plot

The soil in the plot was slightly acidic (mean pH ~5.7 with a range of 3.85–6.63) and had an identifiable pattern as lower pH values (down to pH 3.85) were found in the southwestern part of the plot (Figure S2 and Table S9). The CEC decreased significantly with depth as higher values were found in the surface horizon (~34.5 cmol $^{(+)}$ kg^{-1} *vs.* ~14.7 cmol $^{(+)}$ kg^{-1} at 20 cm depth) while higher CEC values were observed in the north-eastern part of the plot (Table 2, Figure 2 and S3).

	Depth (cm)	CEC	Ca	K	Mg	N	P	Ca/Mg
Total	0–5	-	2490 a (558–10 500)	224 a (60.7–791)	5780 d (1290–25 400)	7.60 (2.40–24.2)	175 b (99.1–253)	-
	5–10	-	1190 b (157–5910)	148 b (43.5–340)	6860 c (1210–26 600)	-	175 b (106–247)	-
	10–15	-	1100 b (61.8–4810)	148 c (3.72–459)	7570 b (1250–35 500)	-	180 a (86.9–230)	-
	15–20	-	686 c (89.3–5670)	145 b (34.3–551)	9400 a (1360–37 100)	-	174 ab (113–302)	-
Exchangeable	0–5	34.5 a (12.8–66.8)	9.11 a (1.00–28.9)	0.52 a (0.17–1.41)	10.4 a (5.35–42.9)	-	-	0.91 a (0.06–3.56)
	5–10	19.4 b (5.39–54.9)	4.08 c (0.17–19.4)	0.30 b (0.10–1.02)	7.51 c (2.2–31.4)	-	-	0.54 b (0.03–3.29)
	10–15	20.9 b (4.12–51.5)	4.31 b (0.48–22.2)	0.29 b (0.10–0.74)	7.89 b (2.41–26.1)	-	-	0.56 b (0.06–3.45)
	15–20	14.7 d (0.68–55.0)	2.00 d (0.06–12.9)	0.19 c (0.06–1.24)	6.15 d (2.48–34.5)	-	-	0.29 c (0.01–2.57)

Table 2. Soil chemistry from the profiles in the plot in the Plaine de Lac (New Caledonia). Concentrations are summarized as median (minimum-maximum). *Footnote: According to the Waller-Duncan means separation test, medians followed by the same letter are not significantly different at the 5% level. All total concentrations are in mg* kg^{-1} *while exchangeable concentrations are in cmol* $^{(+)}$ kg^{-1}.

Significant differences in Ca_{ex} and Ca_{tot} were found according to depth and location, but despite an observable pattern with higher values around the creek, no statistical significance was found (Table 2, Figure 2, 3, S4 and S5). The Ca^{2+} component was responsible for 28.3%, 22.9%, 21.7%, and 13.2% of the total CEC at 5, 10, 15, and 20 cm depths, respectively (Table S10). Almost half of the plot (44.4%) had a Ca_{ex} >10.0 cmol $^{(+)}$ kg^{-1} in the topsoil (0-5 cm), while 8.7% in the intermediary horizons (10 cm and 15 cm depths) and only a negligible part (0.7%) of the deepest horizon exceeded 10 cmol $^{(+)}$ kg^{-1} (Figure 2 and S4).

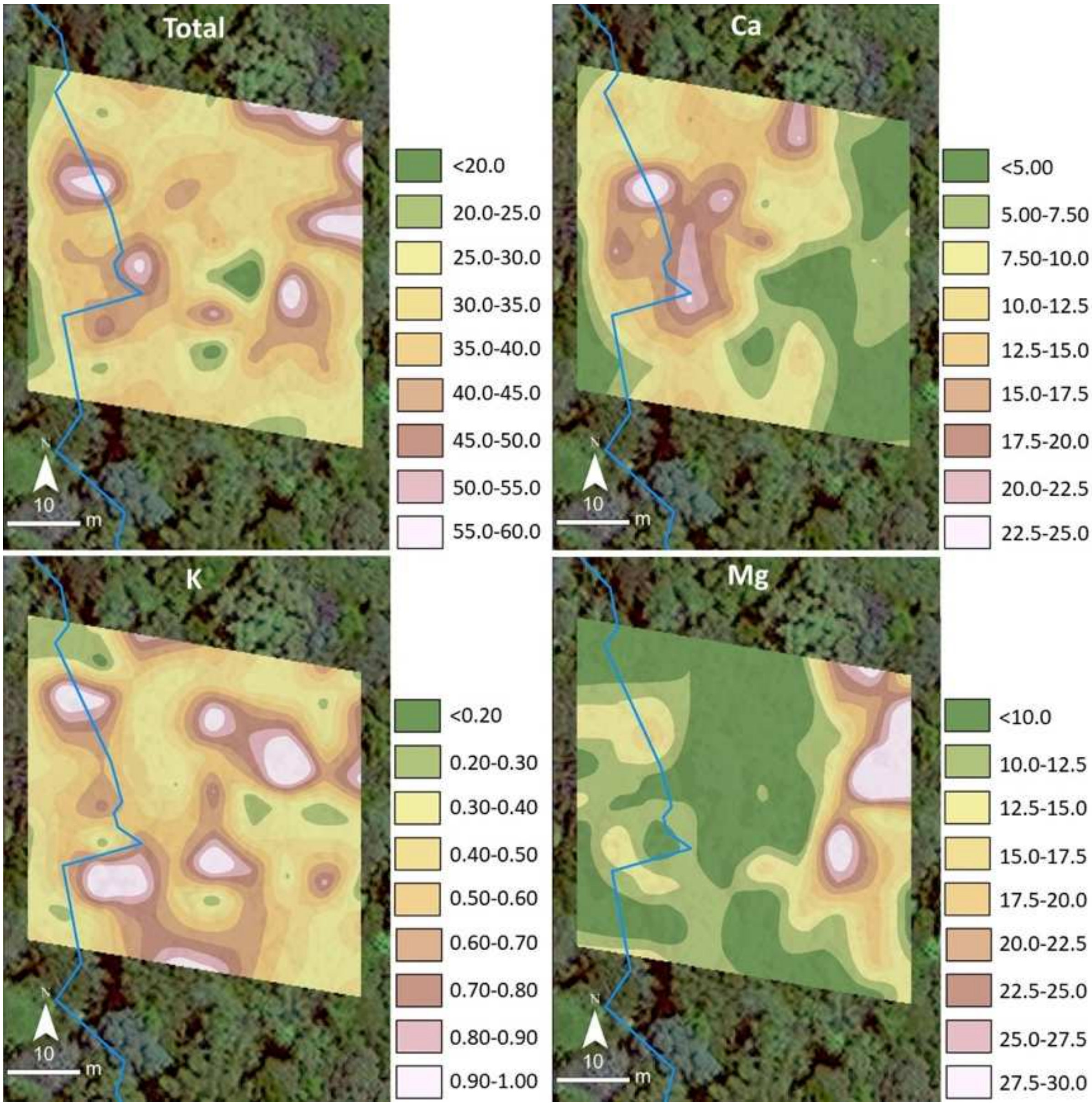

Figure 2. Spatial distribution of CEC and exchangeable cations (cmol $^{(+)}$ kg^{-1}) in topsoil (0-5 cm) across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred (one per subplot) samples.

Calcium pseudo-total concentrations mimicked Ca_{ex} trends with higher concentrations in the surface horizon and around the creek (~3500 compared to ~1000 mg kg^{-1} – Table 2, Figure 3 and S5). Higher K_{ex} values were found in the surface horizons (~0.52 compared to 0.19 cmol $^{(+)}$ kg^{-1}), but the relative importance of K_{ex} to CEC remained stable (~1.5%) through the soil profile while no spatial pattern was observable (Table 2, S10, Figure 2). Pseudo-total concentrations of K mirrored that of K_{ex} with higher concentrations (~220 compared to ~145 mg kg^{-1}) in the top layers of the soil (Table 2, Figure 3). The contribution of Mg_{ex} to the CEC increased significantly with depth (median increased from 31.2 to 49.3%) despite significantly lower Mg_{ex} values in the deeper horizons (Table 2 and S6). Higher values were observed in the northeastern part of the plot in the deeper horizons and around the creek for Mg_{ex} while no defined pattern existed for pseudo-total Mg concentrations which significantly increased with depth (Figure 2, 3, S6 and S7).

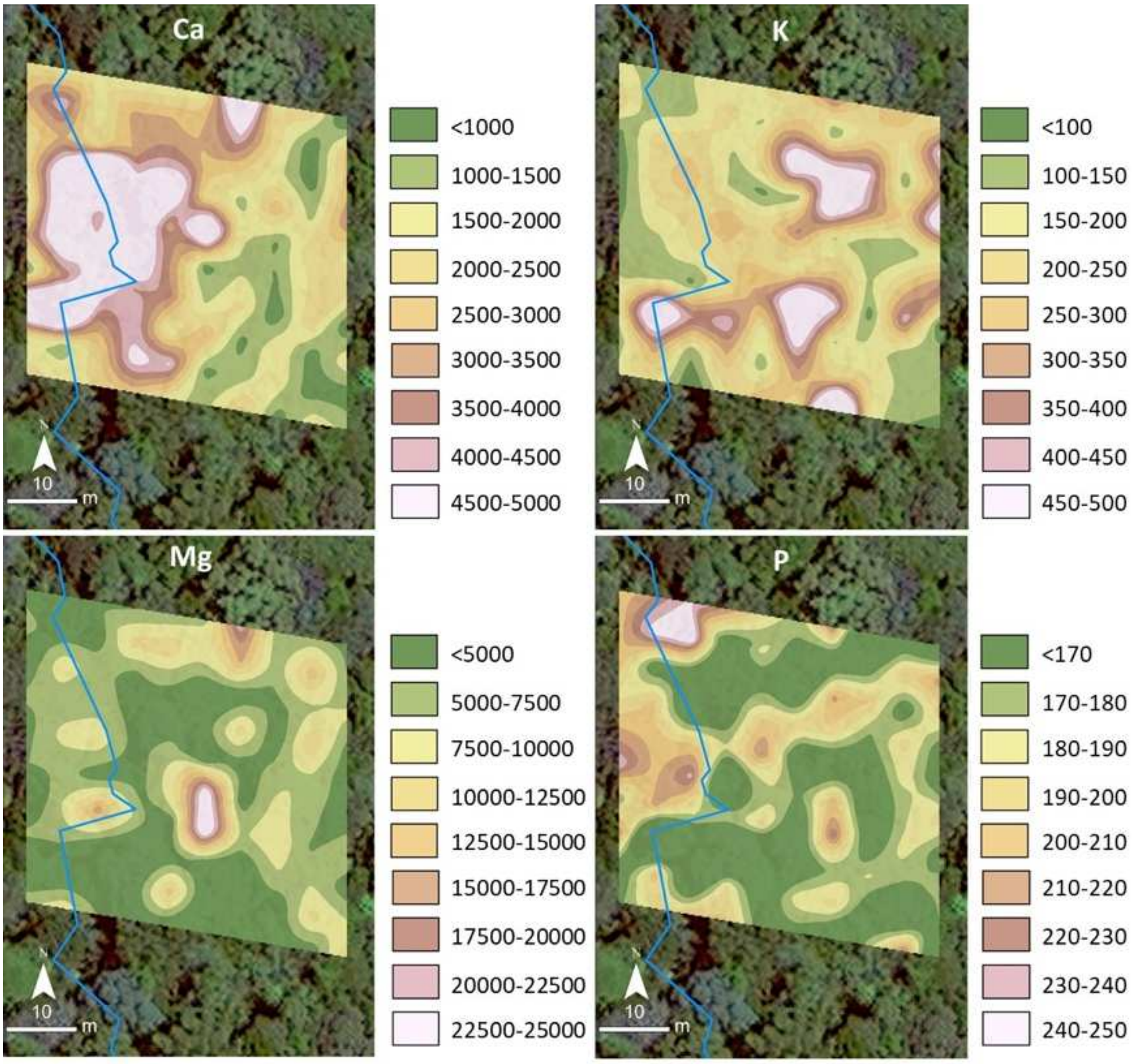

Figure 3. Spatial distribution of pseudo-total concentrations (mg kg^{-1}) in topsoil across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred (one per subplot) samples.

Across the plot, the Ca/Mg ratio decreased with depth (from ~0.91 to ~0.29) while lower values were found in the eastern half of the plot (Table 2 and Figure S8). Unlike the other major nutrients, P distribution was relatively homogeneous with a slight increase through the soil profile and no identifiable spatial pattern (Table 2, Figure 3). Nitrogen concentrations (top 5 cm only) did not show any spatial pattern in the plot with concentrations varying from 2.40 g to 24.2 g N kg^{-1} (Table 2; spatial data not shown).

Quantities of major nutrients in living standing tree biomass and soil

All estimates were calculated based on a biomass of 225 tonnes ha$^{-1,}$ that being ~80% of the total plot biomass (~281 tonnes ha^{-1} when trees >10 cm were included). The total mass was divided as follows: stems ~83.7%, branches ~14.6%, and leaves (old and young leaves) ~1.6%. Trees from the Myrtaceae and Sapotaceae comprised the greatest quantities of total nutrients in the plot due to their high combined biomass (Table S11). In total, the standing biomass was made up of ~470 kg N ha^{-1}, ~3390 kg Ca ha^{-1}, ~1970 kg K ha^{-1}, ~660 kg Mg ha^{-1} and ~87.5 kg P ha^{-1} while the first 20 cm of soil contained ~3900 kg Ca ha^{-1}, 448 kg K ha^{-1}, ~20 500 kg Mg ha^{-1}, and 460 kg P ha^{-1}(Figure 4).

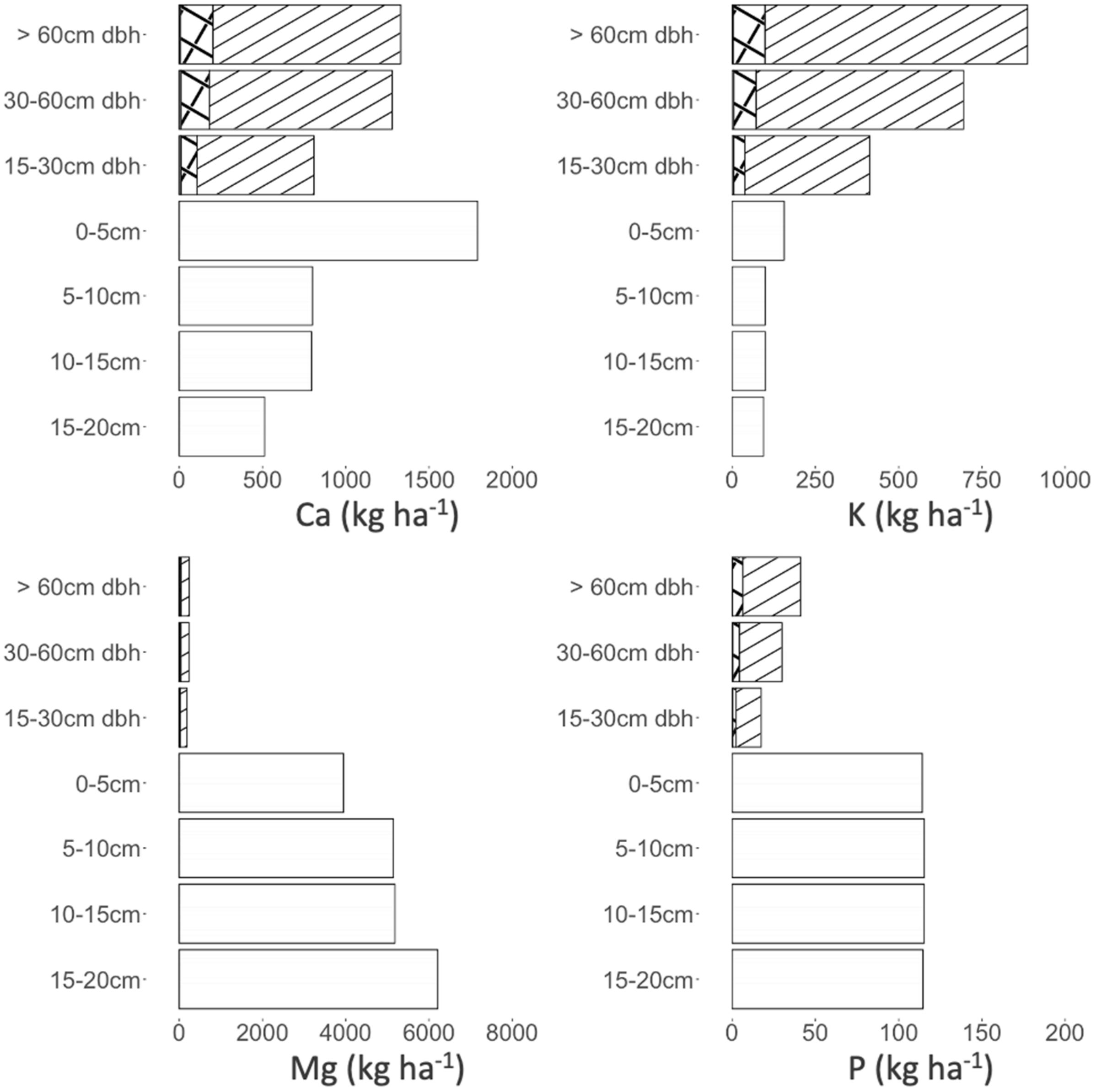

Figure 4. The amounts of calcium, potassium, magnesium, and phosphorus in the above-ground vegetation by components and soils in the tropical forest plot in the Plaine des Lacs, New Caledonia. Stem: thin oblique lines, Branches: grid, Leaves: circles, Soil: blank.

Therefore, K was the only nutrient that was predominantly contained in the standing biomass (~81.5% of total K in the system). About half of the Ca was contained in the standing biomass (~46.5%), while Mg and P were primarily found in the soil (with just ~3.1% and ~16.0% in the standing biomass).

Leaf litterfall and nutrients chemistry

During the one-year study period, around 6.1 tonnes ha^{-1} of litterfall was recorded, depositing approximately ~47 kg ha^{-1} of N, ~80 kg ha^{-1} of Ca, ~11 kg ha^{-1} of K, ~17 kg ha^{-1} of Mg, and ~700 g ha^{-1} of P (Table 3).

Month	Mass	N	Ca	K	Mg	P
Feb 18	1720 (714–4880) a	13.1 (5.29–38.6)	12.7 (2.87–27.5)	1.32 (0.45–3.35)	2.88 (1.28–6.84)	0.18 (0.09–0.37)
Mar 18	435 (0–806) abc	3.02 (0–6.26)	5.61 (1.95–11.3)	0.66 (0.20–1.82)	1.09 (0.55–2.04)	0.05 (0.03–0.12)
April 18	238 (130–419) c	1.47 (0–3.05)	2.77 (0.65–7.25)	0.53 (0–1.37)	0.62 (0.25–1.2)	0.03 (0.01–0.05)
May 18	395 (0–1080) c	2.47 (0–8.44)	5.26 (0–14.5)	0.88 (0–3.98)	0.98 (0–2.59)	0.04 (0–0.10)
Jun 18	93.0 (0–241) d	0.71 (0–2.09)	1.34 (0–5.32)	0.29 (0–1.63)	0.29 (0–0.87)	0.01 (0–0.06)
Jul/Aug 18†	398 (0–1300) c	3.13 (0–8.44)	4.65 (0–11.7)	0.53 (0–1.59)	1.05 (0–2.81)	0.06 (0–0.20)
Sept 18	533 (0–1230) bc	3.54 (0–8.15)	7.27 (0–17.1)	1.21 (0–2.49)	1.76 (0–5.20)	0.07 (0–0.18)
Oct 18	916 (0–1480) abc	6.84 (0–13.1)	10.3 (0–16.9)	2.48 (0–5.12)	2.73 (0–4.52)	0.11 (0–0.17)
Nov/Dec 18†	2250 (924–8060) ab	18.3 (6.84–79.8)	29.9 (10.3–118)	3.36 (1.04–10.1)	6.63 (2.99–27.3)	0.25 (0.06–0.90)
Jan/Feb 19†	830 (0–2720) bc	7.60 (0–46.5)	11.4 (0–44.2)	0.75 (0–1.89)	2.02 (0–4.89)	0.11 (0–0.37)
Total	6090	47..1	78.5	10.7	17.2	0.73

Table 3. Total quantities (kg ha^{-1}) of nutrients returning to the soil via litterfall per month over a one-year period in the Plaine de Lac (New Caledonia). *Footnote: Means followed by the same letter are not significantly different at the 5% level according to the Waller-Duncan means separation test.* † *values are for two months.*

The quantity of litterfall significantly differed depending on the season (Table 3). The greatest quantities were collected in the two months during the ‘hot’ season, whereas the lowest quantities of litterfall were collected during the April to August period, corresponding to the ‘cooler’ season (Table 3).

^{14}C dating of a Pycnandra acuminata tree

The ^{14}C analysis (SUERC-95134) analyses presented uncertainties because of ^{14}C cosmogenic variations (AD 1700–1950 plateau) but it was determined that the sample was at least ~224 years old (or up to ~360 years), suggesting a growth rate between 0.9 mm and 1.5 mm year^{-1}.

DISCUSSION

Ultramafic soils exert selective edaphic pressures as these soils are naturally deficient in two (K and P) of the main nutrients that limit primary production (Brooks 1987, Proctor 2003). Furthermore, these soils have highly imbalanced Ca/Mg quotients, which are toxic to plant species that have not developed adaptations (Echevarria 2021). Calcium was the only element correlated with both family and species importance index, suggesting that a low physiological requirement for Ca gives these species a competitive advantage in this ultramafic system. Other evolutionary adaptations may have conferred certain species competitive advantages, such as in the Ni hyperaccumulator *P. acuminata* (Sapotaceae), a plant species with 23 individuals in the plot, which, by virtue of containing a latex with up to 250 000 mg Ni kg^{-1}, is ostensibly protected from herbivory and developed allopathic functions (Jaffré et al. 1976, 2018). A companion study focused on the biogeochemical cycling of trace elements and the influence of this tree species in the system and revealed, *via* Ni stable isotope analysis, the biotic origins of the Ni present in the soil upper layers highlighting extensive biogenic Ni cycling (Paul et al. 2021).

Although calculation of the nutrients in the biomass may be underestimated (branch nutrient content may not sufficiently reflect the stem nutrient concentrations while stem radial differences may also occur), more than 80% of K was contained in the standing biomass of the forest system feeding the debate around the nature of nutrient limitations in tropical rain forest soils (Meerts 2002, Brearley 2005). Most tropical soils are typically deficient in P (Vitousek 1984; Vitousek and Sanford 1986; Rao et al. 1999), but K is one of the most deficient elements for plants growing on ultramafic soils as shown in the plot (Brooks 1987; Meerts 2002). The total (~200 mg K kg^{-1}) and exchangeable (~0.2 to ~0.5 cmol $^{(+)}$ kg^{-1}) K concentrations in the plot are in the typical range for many tropical ultramafic soils (Table 2).

However, the soil concentration gradient indicated that K predominantly originated from atmospheric deposition, throughfall and litterfall, as might be expected for an extremely weathered soil where most K has been leached (Bruijnzeel 1989; Galey et al. 2017). Although K is highly mobile, it is assumed that a rapid reuptake of K returned to the soil by plant roots and a high resorption efficiency of K contribute to the 'tight' cycling of this element (Chadwick et al. 1999; Maillard et al. 2015, Galey et al. 2017). Atmospheric K inputs in the plot are assumed to be of the same order (~2 and ~20 kg ha^{-1} year^{-1}) as litterfall inputs (Bruijnzeel 1989). In humid tropical systems, Ca, K and Mg atmospheric inputs are typically similar, while atmospheric P inputs tend to be relatively low (Bruijnzeel 1989). Due to logistical difficulties, the nutrient soil inputs *via* stemflow and throughflow were not assessed in this study despite their potential significance as highlighted in a Bornean ultramafic rain forest ecosystem in which both processes were responsible for 53%, 96%, 81% and 70% of Ca, K, Mg and P soil inputs respectively (Tisserand et al. 2021).

The absence of a P soil gradient in the plot indicates fast recycling of available P provided by the litterfall decomposition which supplies ~730 g P ha^{-1} year^{-1} to this system (Table 2). However, the availability of soil P was not determined in this study but the nature of the local soil (*i.e.* strongly weathered and comprised mainly of Aluminum (Al) and Fe-oxides) suggests that a large part of the total P is occluded and therefore unavailable for uptake by plants (Dieter et al. 2010). The solubilization or desorption of poorly available PO_4^{3-} by the soil microbiome may also be important (Oberson and Joner 2005).

Nitrogen did not show any pattern in the plot as no species differences nor soil spatial trends could be observed (Table S8) while the quantity of N returned to the soil via litterfall was well within the range generally observed for tropical forests (Vitousek 1984). Although ultramafic soils have low concentrations of N, both observations suggest that N is not limiting (similarly to most non-ultramafic tropical environments) unlike K and most likely P (Vitousek 1984; Brearley 2005).

Calcium and Mg are not limiting in the plot, but the low Ca/Mg quotient in the plot, especially in the deeper soil layers (0.29) poses edaphic stresses to plants (Table 2). The difference in origins and biogeochemical cycling of these elements become clear when Ca_{ex} and Mg_{ex} values are normalized to the CEC. The relative Mg_{ex} values increase with depth (31.2% to 49.3%), while, in contrast, relative Ca_{ex} values decrease (28.3% to 13.2%). This fact alone suggests a difference in the origin of both elements as Ca is retained in the topsoil horizon and Mg leaches down the soil profile because of different degrees of uptake. The greater Ca_{ex} and Mg_{ex} in the surface horizon of the creek area may indicate that both elements are removed from the system due to runoff (Figure 2, S4 and S6), despite organic matter retention (van der Heijden et al. 2014). The litterfall was enriched in Ca, which can be explained by the mobility of Mg in plants (e.g. active redistribution from old leaves to young leaves) and Ca precipitation to form deposits providing structural support for cell walls (Demarty et al. 1984).

Abiotic and biotic processes continuously (and simultaneously) occur and are responsible for nutrient mobility across ecosystems (*e.g.* uptake and storage in the vegetation, litter production, and decomposition or weathering; Proctor 1987). Although roots play an essential role in many of the fundamental functions of a plant from acquiring nutrients to providing anchorage, most studies to date, including ours, focused on above-ground processes due to the challenging nature of root sampling (Cusack et al. 2021). Hence, despite the undeniable connections between above and below-ground processes, nutrient cycling research including the latter compartment are extremely scarce especially in tropical ecosystems (Vitousek and Sanford 1986, Johnson and Turner 2019). Furthermore, the processes occurring belowground are not only extremely complex and specific but also poorly predictable because of – but not only – the numerous methodological problems still existing nowadays (Vogt et al., 1996; Freschet et al. 2021). Nevertheless, few trends have been observed across the world in nutrient-limited ecosystems including shallow and dense rooting systems adapted to capture nutrients rapidly from litterfall (observed in the plot through indirect observations) or lower shoot:root nutrient ratios (Vitousek and Sanford 1986, Foster and Bhatti 2006, Lambers et al. 2008, Ge et al. 2013, Wurzburger and Wright 2015). Both suggest a great contribution of the belowground compartment in tropical forests nutrient cycling especially in low-fertility soils but processes occurring in ultramafic are both chemically and physically diverse (Brearley, 2005; Echevarria, 2021).

Based on the values of nutrients contained in the biomass (Table S11), the total removal of biomass through logging would empty most stocks of nutrients essential for the existence forest systems. In the plot, it would remove around two tonnes ha^{-1} of the most limiting element (K – Figure 4, Table S11). Future studies should focus on measuring the yearly biomass increments to determine the quantities of each element taken up by plants annually. Nonetheless, it would probably correspond to several centuries of atmospheric deposition. Moreover, clear-felling results in major soil runoff and erosion, which further drastically increases nutrient losses in this ecosystem (Bormann et al. 1968), which would hamper efforts to re-establish forest once cleared. Furthermore, these forests are typically slow growing, as the radiocarbon dating of a large *P. acuminata* in this study demonstrates. *Agathis ovata* (Araucariaceae) occurring on ultramafic soils in the plot area has demonstrated an even slower mean growth rate of 0.5-mm year^{-1}, meaning that trees with a diameter of 30 cm are at least 700 years old (Enright et al. 2003).

This study focused on a rain forest developed over millennia on exceptionally nutrient-poor ultramafic soils, with the results showing how major soil-derived nutrients are cycled in this system. New Caledonia is a biodiversity hotspot of global significance, but its forests are highly threatened, with only 17.5% of the natural vegetation remaining (Sloan et al. 2014). Of 1160 plant species evaluated, 117 species are now critically endangered and ten likely extinct (Bouchet et al. 1995, RLA-NC 2019). Land clearance, bush fires, and mining activities are the leading causes of the New Caledonian vegetation cover disappearance (RLA-NC 2019) and significantly impact rain forest on ultramafic soils (Ibanez et al. 2018).

Although the sampling in this study was extensive, the high complexity of the ecosystem necessitates more detailed measurements collected over a longer period focusing on roots but also tree growth rates and nutrient inputs and outputs to advance a fuller mechanistic understanding of nutrient fluxes in the New Caledonian ultramafic rain forest ecosystems.

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