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

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## HAL Id: hal-03601411
### https://hal.inrae.fr/hal-03601411

Submitted on 22 Jul 2024

1    Title: **Stocks and biogeochemical cycling of soil-derived nutrients in an**

2    **ultramafic rain forest in New Caledonia**

3

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

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38 **CONFLICTS OF INTEREST/COMPETING INTERESTS**

39 The authors declare no conflict of interest.

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**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.

## 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

83 significantly limits its availability (Vitousek et al. 2010). In New Caledonia, this is especially

84 true for substrates derived from ultramafic rocks that are naturally rich in Fe-oxides

85 (Schwertmann and Latham 1986, Quantin et al. 1997). The storage and partitioning of nutrients

86 in rain forest ecosystems are diverse and complex as they occur over a broad range of substrates

87 (Proctor 1987). For example, a study in New South Wales, Australia, comparing 'rich' and

88 'poor' soils showed that specific nutrient utilization varied significantly between localities with

89 lower nutrient availability synonymous with higher nutrient use efficiency (Lambert et al.

90 2016). Nonetheless, little is known about rain forest nutrient flows and nutrient budgets in

91 ultramafic areas because of the complexity and the wide range of mechanisms involved (*e.g.*

92 bedrock weathering, microbial activity) despite the reporting of more and more sophisticated

93 studies (*e.g.* Johnson et al. 2001, Fujii et al. 2011, Nasto et al. 2017).

94

95 The 'biogeochemical niche' hypothesis suggests that multiple plant species thrive in the same

96 ecosystem as a result of a balance in nutrient uses obtained through time to limit competition

97 (*e.g.* growth, uptake, soil space – Garten 1978, Peñuelas et al. 2010, 2019, Urbina et al. 2017).

98 According to Ågren and Weih (2012), plant nutrient concentration differences within

99 ecosystems mainly result from the soil elemental availability diversities. The co-occurrence of

100 these factors, especially in slow-growing plant communities, ultimately leads to extremely

101 complex and diverse plant assemblages. It also possibly explains the high elemental

102 concentrations found in certain species compared to the substrate on which they are growing

103 (van Breemen 1995, Fyllas and Troumbis 2009). Slow-growing species are *de facto* adapted by

104 their low nutrient needs, efficient recycling, and uptake mechanisms to nutrient-limited

105 ecosystems (Chapin 1980).

106

107     Ultramafic soils which develop from the weathering of ultramafic rocks cover ~3% of the

108     Earth's surface. Most ultramafic substrates are highly infertile, but ultramafic substrates and

109     especially Ferralsols are among the most constraining soils for plant growth due to the lack of

110     clay minerals, acidic pH, low CEC, major nutrient deficiencies, and high cobalt (Co), chromium

111     (Cr), manganese (Mn) and nickel (Ni) concentrations (van der Ent et al. 2015, Pillon et al. 2020,

112     Echevarria 2021). One of the largest ultramafic terranes (~5500 $km^2$) occurs in New

113     Caledonia – an archipelago ~1500 km east of Australia in the southern tropical zone north of

114     the Tropic of Capricorn (Maurizot et al. 2020). It is renowned for its exceptional biodiversity

115     with ~3300 vascular plant species, of which ~2100 grow on ultramafic substrates including

116     over 180 metal hyperaccumulator species (Isnard et al. 2016; Gei et al. 2020).

117

118     These plants that may accumulate more than 100 times more of a metal than most other

119     metallophytes and represent one of the best examples of plant adaptation to harsh environments

120     (van der Ent et al. 2013). Two highly discernible vegetation types occur on New Caledonian

121     ultramafic soils: various types of rain forests and the maquis (Jaffré 1980). The presence of

122     some families (*e.g.* Myrtaceae, Rubiaceae) or conifers (Gymnosperms) on ultramafic soils

123     results from the occurrence of specific physiological attributes, which include low foliar P and

124     potassium (K) or the ability to cope with an imbalanced calcium (Ca)/magnesium (Mg) quotient

125     or high concentrations of Ni and Mn in the soil (Jaffré 1980).

126

127     The current study aimed to determine the biogeochemical cycling of nutrients and to establish

128     to what degree these nutrients are 'locked up' in living biomass in a New Caledonian ultramafic

129     forest. To that end, exhaustive sampling was undertaken to calculate the amounts of N, P, K,

130     Ca, and Mg in both standing biomass and soil, as well as the topsoil enrichment and the returns

131 from litterfall. Ultimately, this information will help restore rain forests in New Caledonia

132 where clear-felling has taken place.

133

134 **MATERIALS AND METHODS**

135

136 *Location and condition of the plot and census of tree flora*

137 The study plot (22° 16′29″ S, 166° 54′14″ E; ~270 to ~300 a.s.l) was in the Grand Massif

138 du Sud, one of the world's largest ultramafic massifs which dominates the southern part of

139 Grande Terre in New Caledonia (Figure S1). The local rain forest established over harzburgite

140 bedrock (Table S1) that weathered into a Geric Ferralsol (Becquer et al., 2001). The area is in

141 a tropical oceanic zone with an annual rainfall of ~3300 mm. The climate of New Caledonia is

142 divided into 'hot' and 'cool' seasons (Météo France 2020). The hot season

143 (>300 mm precipitation month$^{-1}$ and mean temperature >28 ℃) lasts from January to April and

144 the cool season (<250 mm precipitation month$^{-1}$ and mean temperature <25 ℃) continues from

145 June to September while transition periods occur in May and later from October to December

146 (Météo France 2020). Plot data were obtained from the rain forest plot network NC-PIPPN

147 established across New Caledonia (Ibanez et al. 2013, Birnbaum et al. 2015). The current study

148 was undertaken in a 0.25-ha subplot located in the center of a 1-ha plot (Figure 1). The 0.25-ha

149 plot was subdivided into 100 subplots (5 m × 5 m).
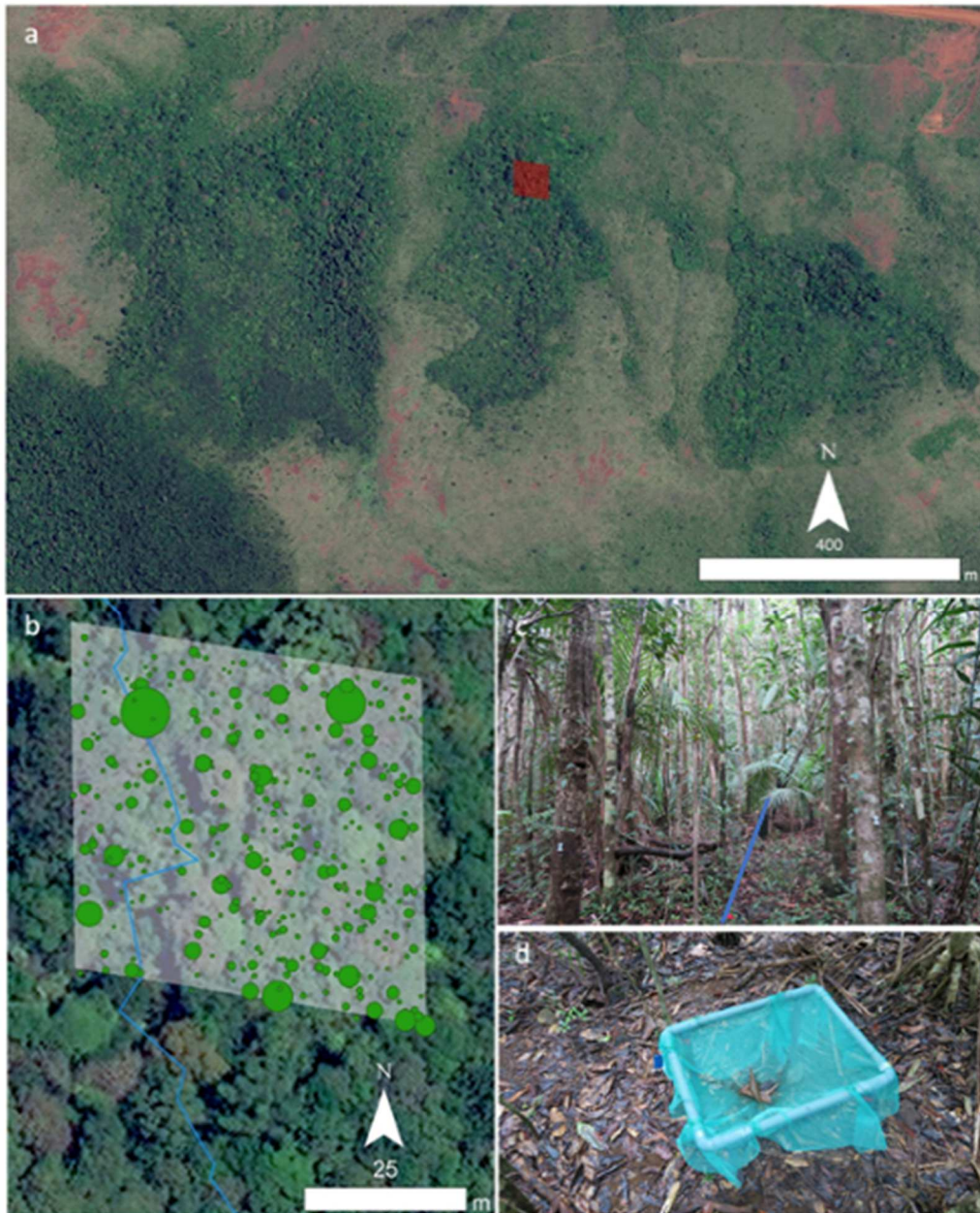
**Figure 1.** Location of the plot and trees in the Plaine de Lac (New Caledonia) and collection
protocol. a: Remnant primary lowland rain forest surrounding the plot. b: Close-up image of
the plot with all the trees overlaying. Worldview-3 imagery. The size of the filled circles
indicates the individual 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.

8

*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

183 (0.01 *M* Ag$^+$) was added. Tubes were then shaken overnight (16–20 h) in the dark and

184 subsequently centrifuged to collect the clear supernatant liquid (Dohrmann 2006). All samples

185 were diluted if needed using ultrapure water (Millipore 18.2 MΩ cm at 25 °C) before analysis

186 *via* Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES; Thermo Scientific

187 iCAP 7400 instrument) in radial mode for Ca, K, Mg and P (Material S1). Soils (top 5 cm only),

188 young leaves and litterfall nitrogen was analyzed using a Vario ELcube (Elementar

189 Analysensysteme GmbH).

190

191 *$^{14}$C analysis of a large Pycnandra acuminata tree*

192 The age of a large individual of *Pycnandra acuminata* (Sapotaceae) was determined to obtain

193 insight into the age of the forest stand. The sampled core for $^{14}$C dating was collected in March

194 2019 using a Haglöf increment borer from one large *P. acuminata* (dbh ~35 cm). The sample

195 was sent to the NEIF Radiocarbon Laboratory for pre-treatment (Material S2) and subsequently

196 on to the Scottish Universities Environmental Research Centre AMS Laboratory for $^{14}$C dating

197 using an NEC accelerator mass spectrometer.

198

199 *Statistical analyses*

200 Statistical analyses were done using version 1.2.5042 of the Rstudio software (PBC). The

201 Waller-Duncan K-ratio t-test was used when data were both normal and homoscedastic. If one

202 of the assumptions was violated, data were transformed to meet both assumptions. A α level of

203 0.05 was used to define statistical significance for each test. Near neighbor interpolations were

204 carried out with ArcMap software (ESRI), version 10.7.1 (2019-06-27) to create the elemental

205 maps. For all families, the family importance value (FIV) was calculated based on the formula

206 developed by Mori et al. (1983). Additionally, the importance value index (IVI) was used to

207 demonstrate the importance of a species in the plot and was defined as the sum of relative

208    frequency, relative dominance, and relative density (Misra 1968). Total plant biomass was

209    calculated *via* the 7$^{th}$ model proposed by Chave et al. (2014), while plant part masses (*i.e.* leaves,

210    branches, stems) were estimated using ratios determined from the tropical rain forest allometric

211    formula proposed by Yamakura et al. (1986). Wood densities were obtained from external

212    organization databases from the literature (*e.g.* ICRAF Database 2019) or in the NC-PIPPN

213    database (Birnbaum et al. 2015). In the absence of value for a species, wood density was

214    extrapolated from the values known for the genus (Chave et al. 2006). Nutrient stocks in

215    biomass were obtained by multiplying tree plant part biomass by the corresponding plant part

216    concentration. Nitrogen concentrations in wood were calculated using the equation: wood N =

217    (0.33 x leaf N) - 0.15 developed from Malaysian tropical forest trees (F. Q. Brearley,

218    unpublished). Nutrient stocks in the soil were obtained by multiplying the concentration in each

219    layer (top 20 cm) by the soil's estimated mass in that layer.

220

221    **RESULTS**

222

223    *Forest floristic diversity and physiognomy of the plot*

224    The 0.25-ha plot had 349 trees in total (189 trees over 15 cm dbh) belonging to 35 families, 52

225    genera, and 64 species, corresponding to a Fisher's alpha of 23.0. Only two families (Myrtaceae

226    and Sapotaceae) had more than three species in the plot with 10 and 6 species, respectively.

227    The Myrtaceae and Sapotaceae also had the highest FIV (42.7 and 36.3), making them the most

228    important families in the plot (Table S2). Seven other families had a FIV >10, with the

229    Sapindaceae (25.8) and Bignoniaceae (15.6) having the largest values while the first nine

230    families accounted for >60% of the overall FIV (Result S1). *Storthocalyx chryseus*

231    (Sapindaceae), *Deplanchea speciosa* (Bignoniaceae), and *P. acuminata* were the three most

232    important species according to the IVI and the most abundant in the plot along with

233    *Sparattosyce dioica* (Moraceae), and *Cunonia balansae* (Cunoniaceae) (Table S3 and

234    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) |  |

235

236 **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

237 as median (minimum-maximum). *Footnote: Medians followed by the same letter are not significantly different at the 5% level according to the*

238 *Waller-Duncan means separation test.*

239    *Concentrations of major nutrients in trees of the plot*

240    Median Ca concentrations varied from 2540 mg Ca kg$^{-1}$ to 13 300 mg Ca kg$^{-1}$ across all tissues,

241    being greatest in twigs and was ~42.7 mg kg$^{-1}$ in xylem sap (Table 1). Of the FIV top 10, the

242    Clusiaceae and Cunoniaceae had the highest Ca concentrations (twigs over 18 000 mg kg$^{-1}$)

243    while Sapindaceae (S. chryseus) had the lowest concentrations (<2000 mg kg$^{-1}$ in twigs) in the

244    plot (Table S4). Young leaves and twigs were significantly enriched in K (>7000 mg kg$^{-1}$)

245    compared to other plant parts (Table 1), while Moraceae, Bignoniaceae and Sapindaceae

246    presented, on average, the highest median K concentrations within the prominent families

247    (Table S5). The median Mg concentrations ranged from 455 mg to 2690 mg kg$^{-1}$ with

248    significantly higher concentrations in the twigs, young leaves, and old leaves (Table 1). Among

249    the main families in the plot, Moraceae had the highest Mg concentrations up to 12 300 mg

250    Mg kg$^{-1}$ in twigs (Table S6). No significant differences in foliar N concentrations were

251    observed across families nor species (Table S7) with concentrations ranging from 4.8 mg to

252    26.4 mg N g$^{-1}$. Median P concentrations varied from 84.5 mg to 347 mg P kg$^{-1}$ in tissues with

253    higher concentrations in young leaves and twigs (> 320 mg P kg$^{-1}$) while xylem sap

254    concentrations were below the limits of detection (ICP reading below 0.10 mg L$^{-1}$) for most

255    species (Table 1). Among the main families, Sapindaceae had significantly higher P

256    concentrations than others (Table S7). Calcium was the only element that was found to be

257    strongly and negatively correlated with both IVI and FIV (p <0.001), while no trends could be

258    observed for the other elements.

259

260    *Soil chemistry of the plot*

261    The soil in the plot was slightly acidic (mean pH ~5.7 with a range of 3.85–6.63) and had an

262    identifiable pattern as lower pH values (down to pH 3.85) were found in the southwestern part

263    of the plot (Figure S2 and Table S9). The CEC decreased significantly with depth as higher

14

264  values were found in the surface horizon (~34.5 cmol$^{(+)}$ kg$^{-1}$ *vs.* ~14.7 cmol$^{(+)}$ kg$^{-1}$ at 20 cm

265  depth) while higher CEC values were observed in the north-eastern part of the plot (Table 2,

266  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) |

267

**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$^{-1}$.*

271    Significant differences in $Ca_{ex}$ and $Ca_{tot}$ were found according to depth and location, but despite

272    an observable pattern with higher values around the creek, no statistical significance was found

273    (Table 2, Figure 2, 3, S4 and S5). The $Ca^{2+}$ component was responsible for 28.3%, 22.9%,

274    21.7%, and 13.2% of the total CEC at 5, 10, 15, and 20 cm depths, respectively (Table S10).

275    Almost half of the plot (44.4%) had a $Ca_{ex}$ >10.0 cmol $^{(+)}$ kg$^{-1}$ in the topsoil (0-5 cm), while

276    8.7% in the intermediary horizons (10 cm and 15 cm depths) and only a negligible part (0.7%)

277    of the deepest horizon exceeded 10 cmol $^{(+)}$ kg$^{-1}$ (Figure 2 and S4).

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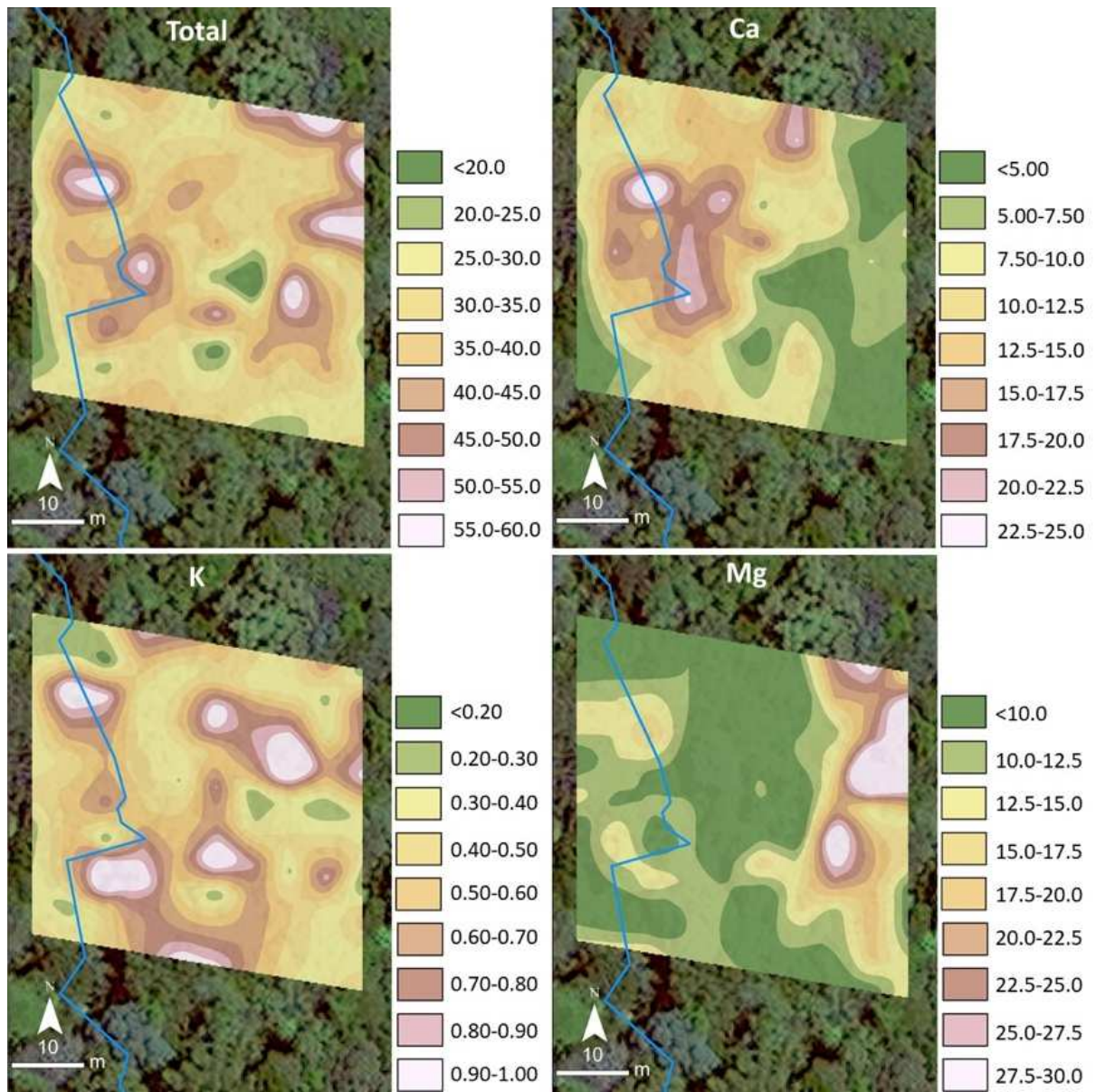
**Figure 2.** Spatial distribution of CEC and exchangeable cations (cmol $^{(+)}$ kg$^{-1}$) in topsoil (0-5 cm) across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred (one per subplot) samples.

285    Calcium pseudo-total concentrations mimicked $Ca_{ex}$ trends with higher concentrations in the

286    surface horizon and around the creek (~3500 compared to ~1000 mg $kg^{-1}$ – Table 2, Figure 3

287    and S5). Higher $K_{ex}$ values were found in the surface horizons (~0.52 compared to 0.19 cmol

288    $^{(+)}$ $kg^{-1}$), but the relative importance of $K_{ex}$ to CEC remained stable (~1.5%) through the soil

289    profile while no spatial pattern was observable (Table 2, S10, Figure 2). Pseudo-total

290    concentrations of K mirrored that of $K_{ex}$ with higher concentrations (~220 compared to

291    ~145 mg $kg^{-1}$) in the top layers of the soil (Table 2, Figure 3). The contribution of $Mg_{ex}$ to the

292    CEC increased significantly with depth (median increased from 31.2 to 49.3%) despite

293    significantly lower $Mg_{ex}$ values in the deeper horizons (Table 2 and S6). Higher values were

294    observed in the northeastern part of the plot in the deeper horizons and around the creek for

295    $Mg_{ex}$ while no defined pattern existed for pseudo-total Mg concentrations which significantly

296    increased with depth (Figure 2, 3, S6 and S7).

297

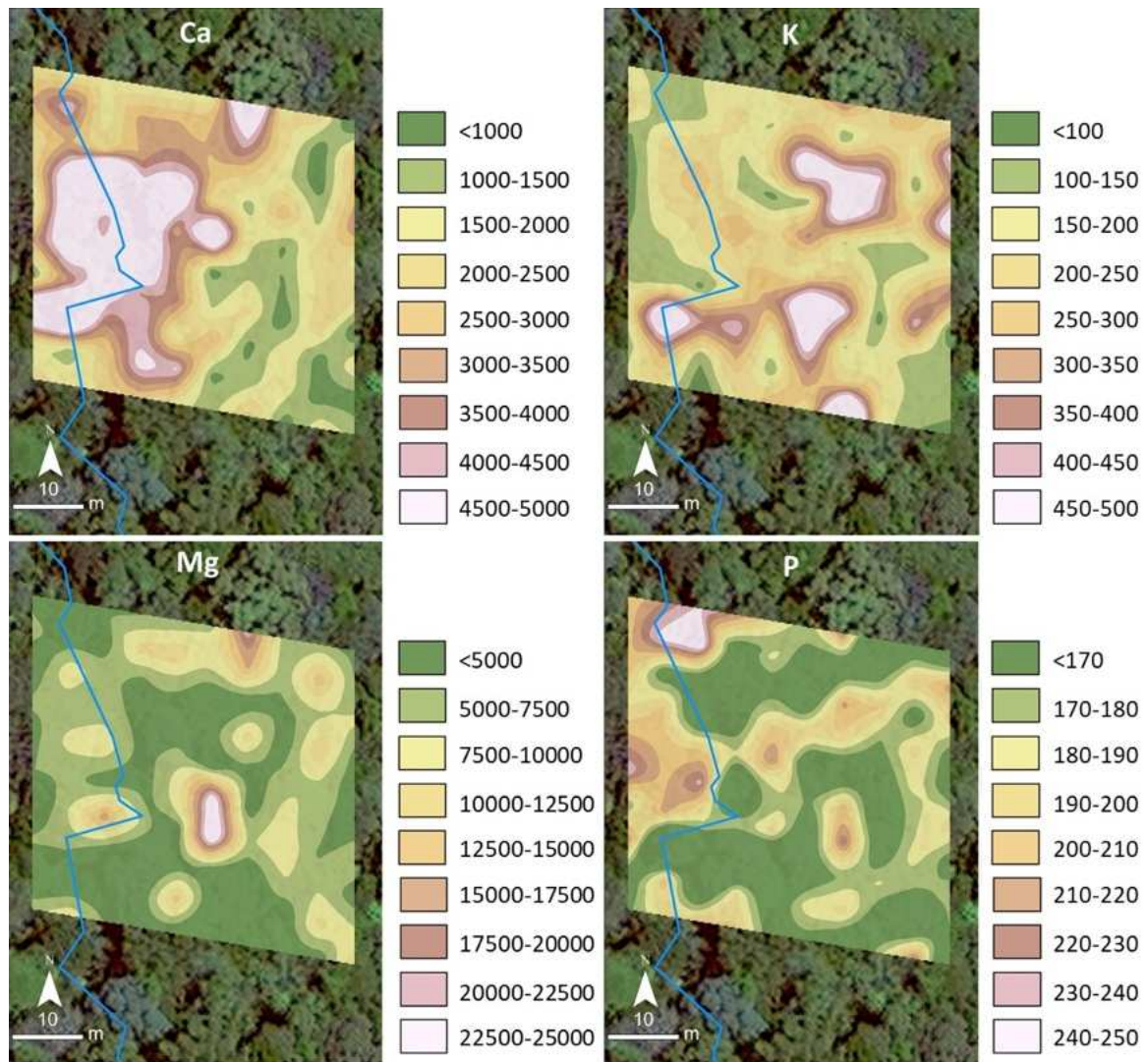**Figure 3.** Spatial distribution of pseudo-total concentrations (mg kg$^{-1}$) in topsoil across the tropical forest plot in the Plaine des Lacs, New Caledonia. The map is based on one hundred (one per subplot) samples.

303 Across the plot, the Ca/Mg ratio decreased with depth (from ~0.91 to ~0.29) while lower values

304 were found in the eastern half of the plot (Table 2 and Figure S8). Unlike the other major

305 nutrients, P distribution was relatively homogeneous with a slight increase through the soil

306 profile and no identifiable spatial pattern (Table 2, Figure 3). Nitrogen concentrations (top 5

307 cm only) did not show any spatial pattern in the plot with concentrations varying from 2.40 g

308 to 24.2 g N $kg^{-1}$ (Table 2; spatial data not shown).

309

310 *Quantities of major nutrients in living standing tree biomass and soil*

311 All estimates were calculated based on a biomass of 225 tonnes $ha^{-1,}$ that being ~80% of the

312 total plot biomass (~281 tonnes $ha^{-1}$ when trees >10 cm were included). The total mass was

313 divided as follows: stems ~83.7%, branches ~14.6%, and leaves (old and young leaves) ~1.6%.

314 Trees from the Myrtaceae and Sapotaceae comprised the greatest quantities of total nutrients in

315 the plot due to their high combined biomass (Table S11). In total, the standing biomass was

316 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

317 P $ha^{-1}$ while the first 20 cm of soil contained ~3900 kg Ca $ha^{-1}$, 448 kg K $ha^{-1}$, ~20 500 kg

318 Mg $ha^{-1}$, and 460 kg P $ha^{-1}$(Figure 4).

319
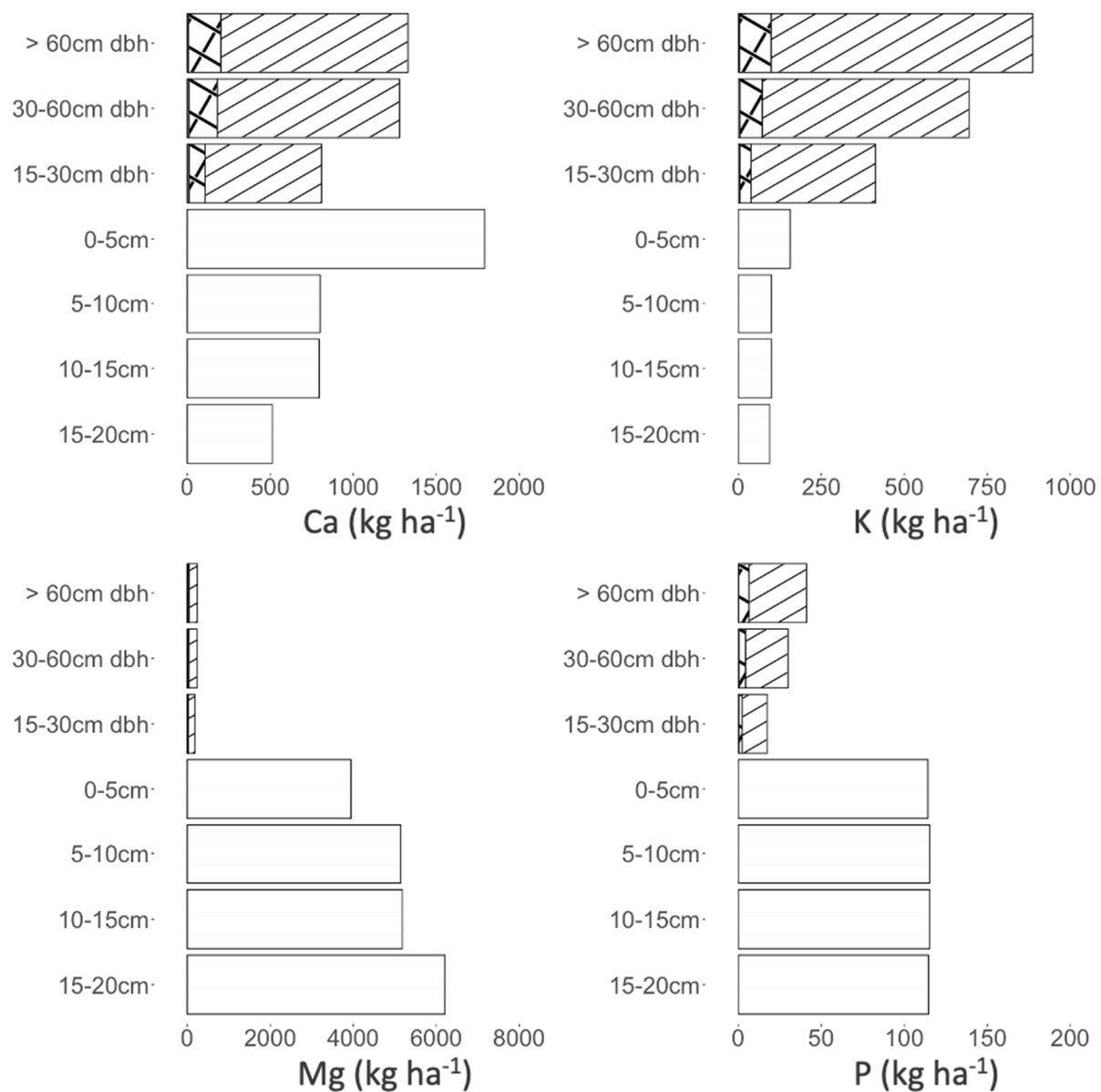
**Figure 4.** The amounts of calcium, potassium, magnesium, and phosphorus in the above-

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.

323

324    Therefore, K was the only nutrient that was predominantly contained in the standing biomass

325    (~81.5% of total K in the system). About half of the Ca was contained in the standing biomass

326    (~46.5%), while Mg and P were primarily found in the soil (with just ~3.1% and ~16.0% in the

327    standing biomass).

328

329    *Leaf litterfall and nutrients chemistry*

330    During the one-year study period, around 6.1 tonnes ha$^{-1}$ of litterfall was recorded, depositing

331    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

332    ~700 g ha$^{-1}$ of P (Table 3).

333

| 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 |

334

335 **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

336 Caledonia). *Footnote: Means followed by the same letter are not significantly different at the 5% level according to the Waller-Duncan means*

337 *separation test. [†] values are for two months.*

338 The quantity of litterfall significantly differed depending on the season (Table 3). The greatest

339 quantities were collected in the two months during the 'hot' season, whereas the lowest

340 quantities of litterfall were collected during the April to August period, corresponding to the

341 'cooler' season (Table 3).

342

343 *$^{14}$C dating of a Pycnandra acuminata tree*

344 The $^{14}$C analysis (SUERC-95134) analyses presented uncertainties because of $^{14}$C cosmogenic

345 variations (AD 1700–1950 plateau) but it was determined that the sample was at least ~224

346 years old (or up to ~360 years), suggesting a growth rate between 0.9 mm and 1.5 mm year$^{-1}$.

347

348

**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).

374    However, the soil concentration gradient indicated that K predominantly originated from

375    atmospheric deposition, throughfall and litterfall, as might be expected for an extremely

376    weathered soil where most K has been leached (Bruijnzeel 1989; Galey et al. 2017). Although

377    K is highly mobile, it is assumed that a rapid reuptake of K returned to the soil by plant roots

378    and a high resorption efficiency of K contribute to the 'tight' cycling of this element (Chadwick

379    et al. 1999; Maillard et al. 2015, Galey et al. 2017). Atmospheric K inputs in the plot are

380    assumed to be of the same order (~2 and ~20 kg ha$^{-1}$ year$^{-1}$) as litterfall inputs

381    (Bruijnzeel 1989). In humid tropical systems, Ca, K and Mg atmospheric inputs are typically

382    similar, while atmospheric P inputs tend to be relatively low (Bruijnzeel 1989). Due to logistical

383    difficulties, the nutrient soil inputs *via* stemflow and throughflow were not assessed in this

384    study despite their potential significance as highlighted in a Bornean ultramafic rain forest

385    ecosystem in which both processes were responsible for 53%, 96%, 81% and 70% of Ca, K,

386    Mg and P soil inputs respectively (Tisserand et al. 2021).

387

388    The absence of a P soil gradient in the plot indicates fast recycling of available P provided by

389    the litterfall decomposition which supplies ~730 g P ha$^{-1}$ year$^{-1}$ to this system (Table 2).

390    However, the availability of soil P was not determined in this study but the nature of the local

391    soil (*i.e.* strongly weathered and comprised mainly of Aluminum (Al) and Fe-oxides) suggests

392    that a large part of the total P is occluded and therefore unavailable for uptake by plants (Dieter

393    et al. 2010). The solubilization or desorption of poorly available $PO_4^{3-}$ by the soil microbiome

394    may also be important (Oberson and Joner 2005).

395

396    Nitrogen did not show any pattern in the plot as no species differences nor soil spatial trends

397    could be observed (Table S8) while the quantity of N returned to the soil via litterfall was well

398    within the range generally observed for tropical forests (Vitousek 1984). Although ultramafic

399    soils have low concentrations of N, both observations suggest that N is not limiting (similarly

400    to most non-ultramafic tropical environments) unlike K and most likely P (Vitousek 1984;

401    Brearley 2005).

402

403    Calcium and Mg are not limiting in the plot, but the low Ca/Mg quotient in the plot, especially

404    in the deeper soil layers (0.29) poses edaphic stresses to plants (Table 2). The difference in

405    origins and biogeochemical cycling of these elements become clear when $Ca_{ex}$ and $Mg_{ex}$ values

406    are normalized to the CEC. The relative $Mg_{ex}$ values increase with depth (31.2% to 49.3%),

407    while, in contrast, relative $Ca_{ex}$ values decrease (28.3% to 13.2%). This fact alone suggests a

408    difference in the origin of both elements as Ca is retained in the topsoil horizon and Mg leaches

409    down the soil profile because of different degrees of uptake. The greater $Ca_{ex}$ and $Mg_{ex}$ in the

410    surface horizon of the creek area may indicate that both elements are removed from the system

411    due to runoff (Figure 2, S4 and S6), despite organic matter retention (van der Heijden et al.

412    2014). The litterfall was enriched in Ca, which can be explained by the mobility of Mg in plants

413    (e.g. active redistribution from old leaves to young leaves) and Ca precipitation to form deposits

414    providing structural support for cell walls (Demarty et al. 1984).

415

416    Abiotic and biotic processes continuously (and simultaneously) occur and are responsible for

417    nutrient mobility across ecosystems (*e.g.* uptake and storage in the vegetation, litter production,

418    and decomposition or weathering; Proctor 1987). Although roots play an essential role in many

419    of the fundamental functions of a plant from acquiring nutrients to providing anchorage, most

420    studies to date, including ours, focused on above-ground processes due to the challenging nature

421    of root sampling (Cusack et al. 2021). Hence, despite the undeniable connections between

422    above and below-ground processes, nutrient cycling research including the latter compartment

423    are extremely scarce especially in tropical ecosystems (Vitousek and Sanford 1986, Johnson

424 and Turner 2019). Furthermore, the processes occurring belowground are not only extremely

425 complex and specific but also poorly predictable because of – but not only – the numerous

426 methodological problems still existing nowadays (Vogt et al., 1996; Freschet et al. 2021).

427 Nevertheless, few trends have been observed across the world in nutrient-limited ecosystems

428 including shallow and dense rooting systems adapted to capture nutrients rapidly from litterfall

429 (observed in the plot through indirect observations) or lower shoot:root nutrient ratios (Vitousek

430 and Sanford 1986, Foster and Bhatti 2006, Lambers et al. 2008, Ge et al. 2013, Wurzburger and

431 Wright 2015). Both suggest a great contribution of the belowground compartment in tropical

432 forests nutrient cycling especially in low-fertility soils but processes occurring in ultramafic are

433 both chemically and physically diverse (Brearley, 2005; Echevarria, 2021).

434

435 Based on the values of nutrients contained in the biomass (Table S11), the total removal of

436 biomass through logging would empty most stocks of nutrients essential for the existence forest

437 systems. In the plot, it would remove around two tonnes ha$^{-1}$ of the most limiting element (K –

438  Figure 4, Table S11). Future studies should focus on measuring the yearly biomass increments

439 to determine the quantities of each element taken up by plants annually. Nonetheless, it would

440 probably correspond to several centuries of atmospheric deposition. Moreover, clear-felling

441 results in major soil runoff and erosion, which further drastically increases nutrient losses in

442 this ecosystem (Bormann et al. 1968), which would hamper efforts to re-establish forest once

443 cleared. Furthermore, these forests are typically slow growing, as the radiocarbon dating of a

444 large *P. acuminata* in this study demonstrates. *Agathis ovata* (Araucariaceae) occurring on

445 ultramafic soils in the plot area has demonstrated an even slower mean growth rate of 0.5-mm

446 year$^{-1}$, meaning that trees with a diameter of 30 cm are at least 700 years old (Enright et al.

447 2003).

448

449　This study focused on a rain forest developed over millennia on exceptionally nutrient-poor

450　ultramafic soils, with the results showing how major soil-derived nutrients are cycled in this

451　system. New Caledonia is a biodiversity hotspot of global significance, but its forests are highly

452　threatened, with only 17.5% of the natural vegetation remaining (Sloan et al. 2014). Of 1160

453　plant species evaluated, 117 species are now critically endangered and ten likely extinct

454　(Bouchet et al. 1995, RLA-NC 2019). Land clearance, bush fires, and mining activities are the

455　leading causes of the New Caledonian vegetation cover disappearance (RLA-NC 2019) and

456　significantly impact rain forest on ultramafic soils (Ibanez et al. 2018).

457

458　Although the sampling in this study was extensive, the high complexity of the ecosystem

459　necessitates more detailed measurements collected over a longer period focusing on roots but

460　also tree growth rates and nutrient inputs and outputs to advance a fuller mechanistic

461　understanding of nutrient fluxes in the New Caledonian ultramafic rain forest ecosystems.

462

463

## REFERENCES

464

465 Ågren, G. I., and M. Weih. 2012. Plant stoichiometry at different scales: element

466       concentration patterns reflect environment more than genotype. New Phytologist

467       194:944–952.

468 Alexou, M., and A. D. Peuke. 2013. Methods for xylem sap collection. Pages 195–207 *In* F. J.

469       M. Maathuis, editor. Plant Mineral Nutrients: Methods and Protocols. Humana Press,

470       Totowa.

471 Bahram, M., F. Hildebrand, S. K. Forslund, J. L. Anderson, N. A. Soudzilovskaia, P. M.

472       Bodegom, J. Bengtsson-Palme, S. Anslan, L. P. Coelho, H. Harend, J. Huerta-Cepas,

473       M. H. Medema, M. R. Maltz, S. Mundra, P. A. Olsson, M. Pent, S. Põlme, S.

474       Sunagawa, M. Ryberg, L. Tedersoo, and P. Bork. 2018. Structure and function of the

475       global topsoil microbiome. Nature 560:233–237.

476 Becquer, T., J. Pétard, C. Duwig, E. Bourdon, R. Moreau, and A. J. Herbillon. 2001.

477       Mineralogical, chemical and charge properties of Geric Ferralsols from New

478       Caledonia. Geoderma, 103:291–306.

479 Birnbaum, P., T. Ibanez, R. Pouteau, H. Vandrot, V. Hequet, E. Blanchard, and T. Jaffré.

480       2015. Environmental correlates for tree occurrences, species distribution and richness

481       on a high-elevation tropical island. AoB Plants 7.

482 Bormann, F. H., G. E. Likens, D. W. Fisher, and R. S. Pierce. 1968. Nutrient loss accelerated

483       by clear-cutting of a forest ecosystem. Science 159:882–884.

484 Bouchet, P., T. Jaffre, and J.-M. Veillon. 1995. Plant extinction in New Caledonia: protection

485       of sclerophyll forests urgently needed. Biodiversity & Conservation 4:415–428.

486 Boyd, R. S. 2007. The defense hypothesis of elemental hyperaccumulation: status, challenges

487       and new directions. Plant and Soil 293:153-176

488 Boyd, R. S., and T. Jaffré. 2001. Phytoenrichment of soil Ni content by *Sebertia acuminata* in

489      New Caledonia and the concept of elemental allelopathy. South African Journal of

490      Science 97:535-538.

491 Brearley, F. Q. 2005. Nutrient limitation in a Malaysian ultramafic soil. Journal of Tropical

492      Forest Science 17:596-609.

493 Brooks, R. R. 1987. Serpentine and Its Vegetation: A Multidisciplinary Approach.

494      Dioscorides Press, Portland.

495 Bruijnzeel, L. A. 1989. Nutrient content of bulk precipitation in south-central Java, Indonesia.

496      Journal of Tropical Ecology 5:187–202.

497 Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin. 1999.

498      Changing sources of nutrients during four million years of ecosystem development.

499      Nature 397:491–497.

500 Chapin, F. S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and

501      Systematics 11:233–260.

502 Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. ter Steege, and C. O. Webb.

503      2006. Regional and phylogenetic variation of wood density across 2456 neotropical

504      tree species. Ecological Applications 16:2356–2367.

505 Chave, J., M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A.

506      Duque, T. Eid, P. M. Fearnside, R. C. Goodman, M. Henry, A. Martínez-Yrízar, W.

507      A. Mugasha, H. C. Muller-Landau, M. Mencuccini, B. W. Nelson, A. Ngomanda, E.

508      M. Nogueira, E. Ortiz-Malavassi, R. Pélissier, P. Ploton, C. M. Ryan, J. G.

509      Saldarriaga, and G. Vieilledent. 2014. Improved allometric models to estimate the

510      aboveground biomass of tropical trees. Global Change Biology 20:3177–3190.

511 Cusack, D. F., Addo-Danso, S. D., Agee, E. A., Andersen, K. M., Arnaud, M., Batterman, S.

512      A., Brearley, F. Q., Ciochina, M. I., Cordeiro, A. L., Dallstream, C., Diaz-Toribio, M.

H., Dietterich, L. H., Fisher, J. B., Fleischer, K., Fortunel, C., Fuchslueger, L.

Guerrero-Ramírez, N. R., Kotowska, M. M., Lugli, L. F., Marín, C., McCulloch, L.

A., Maeght, J.-L. Metcalfe, D. B., Norby, R. J., Oliveira, R. S., Powers, J. S., Reichert,

T., Smith, S. W., Smith-Martin, C. M., Soper, F. M., Toro, L., Umaña, M. N.,

Valverde-Barrantes, O., Weemstra, M., Werden, L. K., Wong, M., Wright, S. J. &

Yaffar, D. (2021) Trade-offs and synergies in tropical forest root traits and dynamics

for nutrient and water acquisition: field and modelling advances. Frontiers in Forests

and Global Change 4, 704469.

Demarty, M., C. Morvan, and M. Thellier. 1984. Calcium and the cell wall. Plant, Cell &

Environment 7:441–448.

Dieter, D., H. Elsenbeer, and B. L. Turner. 2010. Phosphorus fractionation in lowland tropical

rain forest soils in central Panama. Catena 82:118–125.

Dohrmann, R. 2006. Problems in CEC determination of calcareous clayey sediments using

the ammonium acetate method. Journal of Plant Nutrition and Soil Science 169:330–

334.

Echevarria, G. 2021. Genesis and behaviour of ultramafic soils and consequences for nickel

biogeochemistry. Pages 215–238 *In* A. van der Ent, A. J. M. Baker, G. Echevarria,

M.-O. Simonnot, and J. L. Morel, editors. Agromining: Farming for Metals:

Extracting Unconventional Resources Using Plants. Springer International Publishing,

Cham.

Enright, N. J., B. P. Miller, and G. L. W. Perry. 2003. Demography of the long-lived conifer

*Agathis ovata* in maquis and rain forest, New Caledonia. Journal of Vegetation

Science 14:625–636.

Foster, N. W., and J. S. Bhatti. 2006. Forest ecosystems: nutrient cycling. Pages 718–7121 *In*

R. Lal, editor. Encyclopedia of soil science. CRC Press, Boca Raton.

538    Freschet, G.T., L. Pagès, C. M. Iversen, L. H. Comas, B. Rewald, C. Roumet, J. Klimešová,

539        M. Zadworny, H. Poorter, J. A. Postma, and T. S. Adams. 2021. A starting guide to

540        root ecology: strengthening ecological concepts and standardising  root classification,

541        sampling, processing and trait measurements. New Phytologist 232:973–1122.

542    Fujii, K., A. Hartono, S. Funakawa, M. Uemura, Sukartiningsih, and T. Kosaki. 2011.

543        Acidification of tropical forest soils derived from serpentine and sedimentary rocks in

544        East Kalimantan, Indonesia. Geoderma 160:311–323.

545    Fyllas, N. M., and A. Y. Troumbis. 2009. Simulating vegetation shifts in north-eastern

546        Mediterranean mountain forests under climatic change scenarios. Global Ecology and

547        Biogeography 18:64–77.

548    Galey, M. L., A. van der Ent, M. C. M. Iqbal, and N. Rajakaruna. 2017. Ultramafic

549        geoecology of South and Southeast Asia. Botanical Studies 58:18.

550    Garten, C. T. 1978. Multivariate perspectives on the ecology of plant mineral element

551        composition. The American Naturalist 112:533–544.

552    Ge, X., L. Zeng, W. Xiao, Z. Huang, X. Geng, and B. Tan. 2013. Effect of litter substrate

553        quality and soil nutrients on forest litter decomposition: a review. Acta Ecologica

554        Sinica 33:102–108.

555    Guillon, J. H. 1975. Les massifs péridotitiques de Nouvelle-Calédonie : type d'appareil

556        ultrabasique stratiforme de chaîne récente. ORSTOM: Paris.

557    Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology &

558        Evolution 7:336–339.

559    Ibanez, T., E. Blanchard, V. Hequet, G. Keppel, M. Laidlaw, R. Pouteau, H. Vandrot, and P.

560        Birnbaum. 2018. High endemism and stem density distinguish New Caledonian from

561        other high-diversity rainforests in the Southwest Pacific. Annals of Botany 121:25–35.

562  Ibanez, T., J. Munzinger, G. Dagostini, V. Hequet, F. Rigault, T. Jaffré, and P. Birnbaum.

563      2013. Structural and floristic diversity of mixed tropical rain forest in New Caledonia:

564      new data from the New Caledonian Plant Inventory and Permanent Plot Network

565      (NC-PIPPN). Applied Vegetation Science 17:386–397.

566  ICRAF Database. 2019. Worldwide "Open Access" The functional attributes and ecological

567      database. http://db.worldagroforestry.org/.

568  Isnard, S., L. L'huillier, F. Rigault, and T. Jaffré. 2016. How did the ultramafic soils shape the

569      flora of the New Caledonian hotspot? Plant and Soil 403 :53–76.

570  Isnard, S., L. L'huillier, A. L. D. Paul, J. Munzinger, B. Fogliani, G. Echevarria, P.D. Erskine,

571      V. Gei, T. Jaffré, and A. van Der Ent, 2020. Novel insights into the

572      hyperaccumulation syndrome in Pycnandra (Sapotaceae). Frontiers in Plant

573      Science, 11, 559059

574  Jaffré, T. 1980. Étude écologique du peuplement végétal des sols dérivés de roches

575      ultrabasiques en Nouvelle Calédonie. ORSTOM: Nouméa.

576  Jaffré, T., R. R. Brooks, J. Lee, and R. D. Reeves. 1976. *Sebertia acuminata*: a

577      hyperaccumulator of nickel from New Caledonia. Science 193:579–580.

578  Jaffré, T., R. D. Reeves, A. J. M. Baker, H. Schat, and A. van der Ent. 2018. The discovery of

579      nickel hyperaccumulation in the New Caledonian tree *Pycnandra acuminata* 40 years

580      on: an introduction to a Virtual Issue. New Phytologist 218:397–400.

581  Johnson, C. M., I. C. G. Vieira, D. J. Zarin, J. Frizano, and A. H. Johnson. 2001. Carbon and

582      nutrient storage in primary and secondary forests in eastern Amazônia. Forest Ecology

583      and Management 147:245–252.

584  Johnson, D. W., and J. Turner. 2019. Tamm Review: Nutrient cycling in forests: a historical

585      look and newer developments. Forest Ecology and Management 444:344–373.

586 Lambers, H., J. A. Raven, G. R. Shaver, and S. E. Smith. 2008. Plant nutrient-acquisition

587      strategies change with soil age. Trends in Ecology & Evolution 23:95–103.

588 Lambert, M. and J. Turner. 2016. Nutrient distribution and cycling in a subtropical rainforest

589      in New South Wales. Australian Journal of Botany 64:100–110.

590 Maillard, A., S. Diquélou, V. Billard, P. Laîné, M. Garnica, M. Prudent, J.-M. Garcia-Mina,

591      J.-C. Yvin, and A. Ourry. 2015. Leaf mineral nutrient remobilization during leaf

592      senescence and modulation by nutrient deficiency. Frontiers in Plant Science 6:317.

593 Maurizot, P., B. Robineau, M. Vendé-Leclerc, and D. Cluzel. 2020. Chapter 1 Introduction to

594      New Caledonia: geology, geodynamic evolution and mineral resources. Geological

595      Society, London, Memoirs 51:1–12.

596 Meerts, P. 2002. Mineral nutrient concentrations in sapwood and heartwood: a literature

597      review. Annals of Forest Science 59 :713–722.

598 Météo France. 2020. Données publiques de météo-France.

599      https://donneespubliques.meteofrance.fr/.

600 Misra, R. 1968. Ecology Workbook. Oxford & IBH Publishing Company, Calcutta.

601 Mori, S. A., B. M. Boom, A. M. de Carvalino, and T. S. dos Santos. 1983. Ecological

602      importance of Myrtaceae in an eastern Brazilian wet forest. Biotropica 15:68–70.

603 Myers, R. J. K., C. A. Palm, E. Cuevas, I. U. N. Gunatilleke, and M. Brussard. 1994. The

604      synchronisations of nutrient mineralisation and plant nutrient demand. Pages 81–116

605      *In* P. L. Woomer, and M. J. Swift, editors. The biological management of tropical soil

606      fertility. Wiley, Chichester.

607 Nasto, M. K., B. B. Osborne, Y. Lekberg, G. P. Asner, C. S. Balzotti, S. Porder, P. G. Taylor,

608      A. R. Townsend, and C. C. Cleveland. 2017. Nutrient acquisition, soil phosphorus

609      partitioning and competition among trees in a lowland tropical rain forest. New

610      Phytologist 214:1506–1517.

611    Oberson, A., and E. J. Joner. 2005. Microbial turnover of phosphorus in soil. Pages 133–164

612        *In* B. Turner, E. Frossard and D. Baldwin, editors. Organic phosphorus in the

613        environment. CABI Publishing, Wallingford.

614    Paul, A. L. D., S. Isnard, C. M. Wawrick, P. D. Erskine, G. Echevarria, A. J. M. Baker, J. K.

615        Kirkby, and A. van der Ent. 2021. Intensive cycling of nickel in a New Caledonian

616        forest dominated by hyperaccumulator trees. The Plant Journal 107:1040–1055.

617    Peñuelas, J., M. Fernández-Martínez, P. Ciais, D. Jou, S. Piao, M. Obersteiner, S. Vicca, I. A.

618        Janssens, and J. Sardans. 2019. The bioelements, the elementome, and the

619        biogeochemical niche. Ecology 100:e02652.

620    Peñuelas, J., J. Sardans, J. Llusià, S. M. Owen, J. Carnicer, T. W. Giambelluca, E. L.

621        Rezende, M. Waite, and Ü. Niinemets. 2010. Faster returns on 'leaf economics' and

622        different biogeochemical niche in invasive compared with native plant species. Global

623        Change Biology 16:2171–2185.

624    Pillon, Y., T. Jaffré, P. Birnbaum, D. Bruy, D. Cluzel, M. Ducousso, B. Fogliani, T. Ibanez,

625        H. Jourdan, L. Lagarde, A. Léopold, J. Munzinger, R. Pouteau, J. Read, and S. Isnard.

626        2021. Infertile landscapes on an old oceanic island: the biodiversity hotspot of New

627        Caledonia. Biological Journal of the Linnean Society 133:317-341.

628    Proctor, J. 1987. Nutrient cycling in primary and old secondary rainforests. Applied

629        Geography 7:135–152.

630    Proctor, J. 2003. Vegetation and soil and plant chemistry on ultramafic rocks in the tropical

631        Far East. Perspectives in Plant Ecology, Evolution and Systematics 6:105–124.

632    Quantin, P., E. Bourdon, and T. Becquer. 1997. Minéralogie et contraintes édaphiques des

633        sols "ferritiques" dérivés de roches ultrabasiques en Nouvelle-Calédonie : relations

634        entre constituants minéraux et disponiblité en certains éléments (Al, Fe, Si, Mg, Mn,

635        Ni, Co, Cr, Cu, Zn, Mo) facilement solubles. Pages 13–25 *In* T. Jaffré, R.D. Reeves,

636    Becquer, T, editors. Écologie des milieux sur roches ultramafiques et sur sols

637    métallifères : actes de la deuxième conférence internationale sur l'écologie des

638    milieux serpentiniques. ORSTOM, Nouméa.

639  Rao, I., D. Friesen, and M. Osaki. 1999. Plant adaptation to phosphorus limited tropical soils.

640    Pages 61–95 *In* M. Pessarakli, editor. Handbook of plant and crop stress 2nd edition.

641    Marcel Dekker Inc, New York.

642  RLA-NC. 2019. Endemia.nc – Faune et Flore de Nouvelle-Calédonie. https://endemia.nc/.

643  Schwertmann, U., and M. Latham. 1986. Properties of iron oxides in some New Caledonian

644    oxisols. Geoderma 39:105–123.

645  Sloan, S., C. N. Jenkins, L. N. Joppa, D. L. A. Gaveau, and W. F. Laurance. 2014. Remaining

646    natural vegetation in the global biodiversity hotspots. Biological Conservation

647    177:12–24.

648  Tisserand, R., P.N. Nkrumah, A. van der Ent., S. Sumail, B. Zeller, and G. Echevarria. 2021.

649    Biogeochemical cycling of nickel and nutrients in a natural high-density stand of the

650    hyperaccumulator *Phyllanthus rufuschaneyi* in Sabah, Malaysia. Chemoecology 1-15.

651  Urbina, I., J. Sardans, O. Grau, C. Beierkuhnlein, A. Jentsch, J. Kreyling, and J. Peñuelas.

652    2017. Plant community composition affects the species biogeochemical niche.

653    Ecosphere 8:e01801.

654  Van Breemen, N. 1995. Nutrient cycling strategies. Plant and Soil 168:321–326.

655  van der Ent, A., A. J. M. Baker, R. D. Reeves, A. J. Pollard, and H. Schat. 2013.

656    Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant and

657    Soil, 362:319–334.

658  van der Ent, A., T. Jaffré, L. L'Huillier, N. Gibson, R. D. Reeves. 2015. The flora of

659    ultramafic soils in the Australia–Pacific Region: state of knowledge and research

660    priorities. Australian Journal of Botany 63:173–190.

661 van der Ent, A., and D. Mulligan. 2015. Multi-element concentrations in plant parts and fluids

662        of Malaysian nickel hyperaccumulator plants and some economic and ecological

663        considerations. Journal of Chemical Ecology 41:396–408.

664 van Heerwaarden, L. M., S. Toet, and R. Aerts. 2003. Nitrogen and phosphorus resorption

665        efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen

666        fertilization. Journal of Ecology 91:1060–1070.

667 Van der Heijden, G., A. Legout, B. Pollier, J. Ranger, and E. Dambrine. 2014. The dynamics

668        of calcium and magnesium inputs by throughfall in a forest ecosystem on base poor

669        soil are very slow and conservative: evidence from an isotopic tracing experiment

670        (26Mg and 44Ca). Biogeochemistry 118:413–442.

671 Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests.

672        Ecology 65:285–298.

673 Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus

674        limitation: mechanisms, implications, and nitrogen–phosphorus interactions.

675        Ecological Applications 20:5–15.

676 Vitousek, P. M., and R. L. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual

677        Review of Ecology and Systematics 17:137–167.

678 Vogt, K.A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1995.

679        Review of root dynamics in forest ecosystems grouped by climate, climatic forest type

680        and species. Plant and Soil 187:159–219.

681 Wanek, W., S. Drage, N. Hinko-Najera, F. Hofhansl, E. Pölz, R. A, and A. Richter. 2008.

682        Primary production and nutrient cycling in lowland rainforests of the Golfo Dulce

683        region. Pages 155–178 *In* A. Weissenhofer, W. Huber, V. Mayer, S. Pamperl, A.

684        Weber, G. Aubrecht, editors. Natural and Cultural History of the Golfo Dulce Region.

685        Stapfia, Linz.

686    Wang, Y., R. Kanipayor, and I. D. Brindle. 2013. Rapid high-performance sample digestion

687           for ICP determination by ColdBlockTM digestion: part 1 environmental samples.

688           Journal of Analytical Atomic Spectrometry 29:162–168.

689    Wurzburger, N., and S. J. Wright. (2015). Fine-root responses to fertilization reveal multiple

690           nutrient limitation in a lowland tropical forest. Ecology 96:2137–2146.

691    Yamakura, T., A. Hagihara, S. Sukardjo, and H. Ogawa. 1986. Aboveground biomass of

692           tropical rain forest stands in Indonesian Borneo. Vegetatio 68:71–82.