Vertical profiles of leaf photosynthesis and leaf traits, and soil nutrients in two tropical rainforests in French Guiana before and after a three-year nitrogen and phosphorus addition experiment

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34 **Abstract.** Terrestrial biosphere models typically use the biochemical model of Farquhar, von Caemmerer and Berry (1980) to
35 simulate photosynthesis, which requires accurate values of photosynthetic capacity of different biomes. However, data on
36 tropical forests are sparse and highly variable due to the high species diversity, and it is still highly uncertain how these tropical
37 forests respond to nutrient limitation in terms of C uptake. Tropical forests often grow on phosphorus (P)-poor soils and are,
38 in general, assumed to be P- rather than nitrogen (N)-limited. However, the relevance of P as a control of photosynthetic
39 capacity is still debated. Here, we provide a comprehensive dataset of vertical profiles of photosynthetic capacity and important
40 leaf traits, including leaf N and P concentrations, from two three-year, large-scale nutrient addition experiments conducted in
41 two tropical rainforests in French Guiana. These data present a unique source of information to further improve model
42 representations of the roles of N, P, and other leaf nutrients, in photosynthesis in tropical forests. To further facilitate the use
43 of our data in syntheses and model studies, we provide an elaborate list of ancillary data, including important soil properties
44 and nutrients, along with the leaf data. As environmental drivers are key to improve our understanding of carbon (C)-nutrient
45 cycle interactions, this comprehensive dataset will aid to further enhance our understanding of how nutrient availability
46 interacts with C uptake in tropical forests. The data are available at DOI 10.5281/zenodo.5638236 ~~10.5281/zenodo.4719242~~
47 (Verryckt, 2021).

1 Introduction

49 Tropical forests play a significant role in the global carbon (C) cycle, contributing more than one third of global terrestrial
50 gross primary productivity (GPP) (Beer et al., 2010; Malhi, 2010). To obtain accurate estimations of the global C budgets, a
51 thorough understanding of the functioning of these tropical forests is thus important. It is still highly uncertain how these
52 tropical forests, and in particular lowland tropical forests, respond to nutrient limitation and to global change in terms of C
53 uptake (Fleischer et al., 2019; Wieder et al., 2015).
54 Leaf photosynthetic capacity is the primary driver of C uptake and its accurate representation in terrestrial biosphere models
55 (TBMs) is essential for robust projections of C stocks and fluxes under global change scenarios. Photosynthesis in C_3 species
56 is typically represented in nearly every major large-scale TBM by the Farquhar, von Caemmerer and Berry (FvCB) model of
57 photosynthesis (Farquhar et al., 1980; von Caemmerer and Farquhar, 1981).
58 The FvCB model determines photosynthesis (*A*) by the most limiting of two processes, Rubisco activity and electron transport.
59 Empirical studies to determine the key parameters of these two processes (i.e. the maximum rate of carboxylation V_{cmax}, the
60 maximum electron transport rate, J_{max}) and to test empirically their limitations on the leaf- and canopy-scale are necessary for
61 obtaining the data required for parameterizing the FvCB model (Medlyn et al., 2015). Plant trait databases, now widely
62 available, offer an excellent opportunity for parameterizing models. However, data on tropical forests are sparse and highly
63 variable due to the huge species diversity (Rogers, 2014).
64 Moreover, empirical studies on leaf photosynthesis and leaf traits in tropical forests have mainly focused on upper canopy
65 leaves (i.e. Bahar et al. (2016), Berry and Goldsmith (2020), Rowland et al. (2015)) as a trade-off to cover a broader set of tree

species in these highly diverse tropical forests. Subsequently, light and leaf nitrogen (N) profiles are used to upscale leaf- to canopy-level photosynthesis, as is also common practice in temperate and boreal forests (Bonan, 2015). However, the leaf N gradient is shallower than the light gradient (Bonan, 2015) and accumulating evidence suggests a regulating role of phosphorus (P) for photosynthesis in tropical trees growing on low-P soils (Walker et al., 2014; Mo et al., 2019; Norby et al., 2017; Bahar et al., 2016). Consequently, vertical variation in leaf traits within the canopy of tropical forests is often not accounted for in a proper way by TBMs.

Environmental drivers are key to improve our understanding of C-nutrient cycle interactions and our ability to model them. Climate data are often directly available at high spatial resolution and at the global scale from databases such as Worldclim (Ruiz-Benito et al., 2020), while observations of soil properties and soil nutrient availability are often missing (Vicca et al., 2018). Soil variables have been shown to be strong predictors of leaf traits in higher plants (Maire et al., 2015). Comprehensive soil data, including soil properties such as texture and pH as well as important nutrients, are needed to further enhance our understanding of how and why nutrient availability interacts with C uptake in tropical ecosystems and their responses to global environmental change (Vicca et al., 2018).

As most tropical forests are growing on highly weathered soils and contain N-fixing plants and free-living organisms, the widely accepted ecological paradigm states that they tend to be limited by P rather than by N (Wright et al., 2018; Walker and Syers, 1976). Nutrient addition experiments are a great asset to offset possible nutrient limitations and to see how the system reacts (Vitousek and Howarth, 1991). Long-term nutrient addition experiments are important to study the role of leaf nutrients in key role processes such as photosynthesis. However, in tropical forests only a few large-scale nutrient addition experiments have been carried out and the results are ambiguous (Wright et al., 2018; Wright, 2019).

Here, we provide photosynthesis data and a set of leaf traits collected at multiple canopy levels at two forest sites in French Guiana, as well as data on responses to two three-year, large-scale N and P nutrient addition experiments. Given the importance of ancillary data such as environmental data and soil properties for model and synthesis studies (Vicca et al., 2018), we also provide an extensive dataset of environmental data, including pre-treatment soil properties and nutrients.

2 Sampling sites

2.1 Study site description

The data were collected in French Guiana, South America at two old-growth, lowland tropical rainforest sites, Paracou and Nouragues (Figure 1A, B). The climate in French Guyana is tropical wet, characterized by a wet and a dry season due to the north-south movement of the Inter-Tropical Convergence Zone (ITCZ) (Bonal et al., 2008). From December to July, the ITCZ brings heavy rains, which peak in May when monthly rainfall typically exceeds 600 mm. The dry season, with < 100 mm rainfall each month, lasts from August to November, with an additional short, dry period in March. Mean annual air temperature is near 26°C for both sites (Bongers et al., 2001; Gourlet-Fleury et al., 2004).

97　The first study site was situated at the Paracou Research Station (5°16′N, 52°54′W) (Figure 1B, D) and is characterized by an
98　average annual rainfall of 3100 mm year^{-1} (2004 – 2015) (Aguilos et al., 2019). The average density of trees with a diameter
99　at breast height (DBH) > 10 cm is ca. 620 trees ha^{-1}, and tree species richness averaged ca. 160 species ha^{-1} (Bonal et al., 2008).
100　The mean canopy height was 35 m, with emergent trees exceeding 40 m. The second study site, the Nouragues Research
101　Station (4°02′N, 52°41′W) (Figure 1B, C), is located 120 km south of Cayenne. Here we sampled at two locations, near the
102　Inselberg station (Petit Plateau) and near the Pararé station (COPAS). The Nouragues forest receives approximately
103　3000 mm rain year^{-1} and tree density (DBH > 10 cm) averaged ca. 535 trees ha^{-1} (Bongers et al., 2001). Tree species richness
104　ranges between 180 and 200 species ha^{-1}. The canopy height varies between 30 and 40 m, with emergent trees reaching 60 m
105　(Van Der Meer et al., 1998).
106　The soils at Paracou are derived from the Bonidoro series, characterized by schist and sandstones and locally crossed by veins
107　of pegmatite, aplite and quarsites (Gourlet-Fleury et al., 2004; Epron et al., 2006), whereas the soils of Nouragues have a
108　weathered granite parent material of the Caraibe series (van der Meer and Bongers, 1996; Bongers et al., 2001). According to
109　the USDA texture classification chart, the soils at Paracou range from loamy sand to sandy loam and at Nouragues from sandy
110　loam to silty clay (Van Langenhove et al., 2019). These old and highly weathered soils at both sites are characterized as
111　nutrient-poor Acrisols (FAO, 1998) and are, compared to the generally younger, nutrient-richer soils of western Amazonia,
112　particularly low in P concentration (Table 1**Error! Reference source not found.**) (Hammond, 2005; Grau et al., 2017).
113　At both forest sites, an instrumentation tower is in place at which meteorological measurements and measurements of
114　ecosystem net CO_2 exchange with the eddy covariance technique have been carried out on a continuous basis since 2003 in
115　Paracou (Bonal et al., 2008) and since 2014 at Nouragues. The monthly rainfall data measured at the instrumentation towers
116　of Paracou and Nouragues are shown in the dataset.

117　**2.2 Nutrient addition experiment**

118　**2.2.1 Set-up**

119　In 2015, we set up twelve 50 x 50 m plots, in three blocks of four plots, along a toposequence at Paracou and Nouragues,
120　resulting in a total of 24 plots. These blocks were located at distinct landscapes: (1) bottom, i.e. just above the creek running
121　through the valley, (2) slope, i.e. the intermediate section of the elevation and (3) top, i.e. where the slope evens out and
122　becomes the hilltop (Courtois et al., 2018). The valley bottoms and hilltops differ ca. 20–50 m in elevation over horizontal
123　distances of 200–400 m (Van Langenhove et al., 2019), with maximum altitudes of ca. 70 m and 120 m for Paracou and
124　Nouragues, respectively (Courtois et al., 2018).
125　In October 2016, a field nutrient addition experiment at both sites was initiated and is ongoing to this day. In each block, one
126　plot served as control plot and the remaining three plots received one of three nutrient addition treatments (+N, +P or +NP).
127　Fertilizer was applied twice per year by hand-broadcasting commercial urea ((NH_2)$_2$CO) and/or triple superphosphate
128　(Ca(H_2PO_4)$_2$) at a rate of 125 kg N ha^{-1} y^{-1} (+N treatment) or 50 kg P ha^{-1} y^{-1} (+P treatment), or both amounts together (+NP

129 treatment). These application rates are identical as those in the ongoing nutrient addition experiment in Barro Colorado Nature
130 Monument in Panama, which was initiated in 1998 (Wright et al., 2011), and the Amazon Fertilization Experiment (AFEX)
131 near Manaus in Brazil, initiated in 2017 (Lugli et al., 2021), to enable future comparison of our results. In Paracou, these rates
132 of nutrient addition represent, respectively, 130% and 250% of yearly N and P input through litterfall and atmospheric
133 deposition combined (Van Langenhove et al., 2020b).

134 Leaf and soil sampling took place before (in 2015) and after a three-year period (in 2019) of the nutrient addition experiment.
135 To avoid border effects of the nutrient addition, these measurements were conducted in the central 20 x 20 m area within the
136 larger 50 x 50 m plots.

137 **2.2.2 Fertilizer composition**

138 Within the nutrient addition experiment, N was added as commercial urea ($(NH_2)_2CO$) and P as triple superphosphate
139 ($Ca(H_2PO_4)_2$). The chemical composition of the applied fertilizers was analyzed to know the exact composition. Samples of
140 both fertilizers were dried at 70°C for 48 h, after which they were ground. Total N of the fertilizers was determined by dry
141 combustion using a Skalar Primacs (Skalar Holding, The Netherlands). P_2O_5 and MgO in mineral acid where determined by
142 an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany). The ground samples were analyzed
143 with an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany) to determine the potassium (K),
144 calcium (Ca) and magnesium (Mg) concentrations, as well as the heavy metal concentrations (arsenic (As), cadmium (Cd),
145 chromium (Cr), copper (Cu), iron (Fe), nickel (Ni), lead (Pb), zinc (Zn), molybdenum (Mo)).

146 **3 Data and Methods: soil sampling**

147 **3.1 Sampling design**

148 In 2015, we sampled soil to a depth of 30 cm, according to a five-on-dice sampling pattern within the 20 x 20 m plots (Figure
149 2). At each sampling point, we sampled bulk density at a depth of 0-15 cm and 15-30 cm using an auger with a 15-cm long
150 cylindrical head (8-cm diameter). Additionally, we took three soil cores with a gouge auger (30-cm length, 5-cm diameter).
151 These three cores were split into two depths (0-15 cm and 15-30 cm), pooled together per depth and used for gravimetric soil
152 water content determination, soil particle size distribution analysis and chemical analysis after sieving (< 2 mm). We divided
153 the soil into a 'surface' layer (0–15 cm) and a 'deeper' layer (15–30 cm) instead of sampling by generic horizon because the
154 upper horizon at both sites varies between 0–15 and 0–20 cm depth while the next horizon often extends to 50 cm depth and
155 beyond (Van Langenhove et al., 2020c; Guitet et al., 2016; Bongers et al., 2001). In 2019, after 3 years of nutrient addition,
156 the soil sampling was repeated. However, these data have not been processed yet and will be made available through
157 publication as soon as possible.

3.2 Soil physical properties

3.2.1 Bulk density

We sampled soil bulk density in the wet season of 2015. In each plot, we took five cores at two depths and these samples were sieved through a 2-mm sieve. We collected the soil fraction, the roots and the stones, which were dried and weighed separately at 105°C for 24 h. In our database, we report two measures of bulk density: inclusive bulk density is the weight of the dried soil core divided by its volume (i.e. the volume of the auger, 754 cm³), whereas exclusive bulk density is calculated by dividing the total weight of the soil fraction (excluding roots and stones) by the volume of the entire core (i.e. 754 cm³).

3.2.1 Soil particle size distribution

The particle size distribution at plot level was analysed only in the wet season of 2015, assuming it would not change with seasonality. Therefore, we mixed by hand the five samples per plot that were sieved (< 2 mm) after extraction using a gouge auger, and analyzed these mixed samples as one composite sample per depth and per plot. We determined the soil particle size distribution using sedimentation with the hydrometer method (Gee and Bauder, 1986) after SOM oxidation with H_2O_2, as described in protocol 1.3.5 Soil texture in the Supporting information S1 Site characteristics and data management in Halbritter et al. (2020). Soil particles were dispersed with sodium hexametaphosphate and the quantity of sand, silt and clay were determined using a hydrometer.

3.2.3 Soil moisture

The gravimetric soil water content (%) was determined in both the wet and the dry season of 2015. We weighed roughly 10 g of fresh soil, which was then dried at 70°C to constant mass and weighed to obtain the dry mass. The gravimetric water content is calculated as the mass of water (i.e. the difference in mass weight of fresh and dried soil) per mass of dry soil.

3.3 Soil nutrients

3.3.1 Chemical analyses: concentrations and availability

Freshly sieved soil was used for the measurement of pH and the extraction of inorganic N (N_i) and inorganic P (P_i). We measured the soil pH using a pH meter (HI 2210-01, Hanna Instruments, USA) after adding 1M KCl to the soil in a 1:2.5 w:v ratio and shaking it for 1 h. The same solution was passed through a 42-μm filter and the filtrate's concentration of NH_4^+ and NO_3^- was determined colourimetrically (SAN++ continuous flow analyzer, Skalar Inc., The Netherlands). The P_i was extracted with the Olsen-P bicarbonate extraction (Olsen et al., 1954) and measured on an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany).

Sieved soil samples were dried at 60°C to constant mass and was then ground in a ZM 200 ball mill (Retsch GmbH, Haan, Germany). We extracted P_i on previously dried soil with the Bray P acid fluoride extraction (Bray and Kurtz, 1945) followed

187 by analysis on an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany). Water soluble

188 molybdate (MoO_4^{2-}) and phosphate (PO_4^{3-}) were determined through resin extraction on previously dried (60°C) soil

189 (Wurzburger et al., 2012). The soil samples were mixed with water in a 1:6 ratio and five 2-cm² strips of anion-exchange

190 membrane (VWR Chemicals, USA) were added (Van Langenhove et al., 2019; Wurzburger et al., 2012). After stirring this

191 mixture 24 h, the strips were rinsed and eluted with 10% HNO_3. The concentrations of water soluble MoO_4^{2-} and PO_4^{3-} were

192 analyzed with an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany).

193 Additionally, we analyzed total macro- and micronutrient concentrations on previously dried soil. Soil C and N concentrations

194 were determined by dry combustion with a Flash 2000 elemental analyzer (Thermo Fisher Scientific, Germany), and total soil

195 C and N was analyzed by EA-IRMS (EA1110, CE Instruments, Milan, Italy), coupled to a Finnigan MAT Delta Plus IRMS

196 (Thermo Fisher Scientific, Germany). The concentrations of P, K, Ca, Mg, sulphur (S), manganese (Mn), sodium (Na),

197 vanadium (V), strontium (Sr), As, Cd, Cr, Cu, Fe, Ni, Pb, Zn and Mo were obtained by acid digestion in an ultraWAVE

198 digestor (Milestone, Italy), followed by ICP-MS (7500ce model, Agilent Technologies, Tokyo, Japan) analysis.

3.3.2 PRS probes

200 We used Plant Root Simulator (PRS ®) probes (Western Ag ~~Enterprises~~Innovations, Inc., Saskatoon, CA) to provide proxies

201 for plant available ions in soil solution (Van Langenhove et al., 2020a; Halbritter et al., 2020). These PRS probes are ion

202 exchange resin membranes (IEM; approximately 5.5 cm × 1.6 cm, or 17.5 cm² including both sides of the IEM) held in plastic

203 supports that were vertically inserted into soil with minimal disturbance (Hangs et al., 2004). In each plot, we installed five

204 root exclusion cylinders (REC) following a five-on-a-dice design to study soil nutrient dynamics in absence of the root system

205 (Van Langenhove et al., 2020a). RECs were PVC collars inserted 20 cm into the soil to sever all near-surface roots and

206 mycorrhizal fungal hyphae, and were installed prior to the first soil nutrient measurements in May 2015.

207 In both the wet (May) and dry (October) season of 2015, we installed four anion and four cation probes, which formed one

208 sample, into each REC. After a period of two weeks, the PRS^{TM} probes were removed from the soil, washed with distilled

209 water and shipped to the manufacturer for analysis of the following nutrients: P, K, Ca, Mg, S, Mn, Cd, Cu, Fe, Pb, Zn, nitrate

210 (NO_3), ammonium (NH_4), boron (B) and aluminium (Al). In situ burial of the PRS^{TM} probes provide a dynamic measure of

211 nutrient flux, or nutrient supply rate to an ion sink (Gibson et al., 1985; Casals et al., 1995). The results are thus expressed as

212 the amount of nutrient adsorbed per surface area of IEM during the duration of burial (Qian and Schoenau, 2002). In our study

213 it was expressed as µg nutrient 10 cm^{-2}·for two weeks.

4 Data and Methods: leaf sampling

4.1 Tree selection

216 In each 20 x 20 m plot at Paracou and Nouragues, we selected five mature trees, of which three were top-canopy species likely

217 dominating the functioning of the plot and two trees were sub-canopy species. Additionally, we selected twelve trees at the

218   COPAS site near the Pararé station at Nouragues. At Paracou we selected in each 50 x 50 m plot four species of saplings,
219   defined as a tree < 2 m in height, with at least ten individuals per plot. This resulted in seven sapling species selected in total
220   and 40 individuals selected per plot. Overall, we selected 131 trees belonging to 76 different tree species differing in relative
221   abundance (Figure 3, Table 2).

222   **4.2 Photosynthesis**

223   **4.2.1 Leaf gas exchange**

224   We measured leaf gas exchange measurements using a set of infrared gas analyzers (IRGAs) incorporated into a portable
225   photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, USA). A leaf was clamped within a chamber with controlled
226   microenvironmental conditions during the measurements and the device measures the concentration changes of water vapour
227   (H_2O) and carbon dioxide (CO_2) between incoming and outgoing air. The relative humidity inside the chamber (67.9 % $\pm$ 0.06)
228   was kept as close to ambient as possible during the measurements and the air flow rate was set at 500 µmol s^{-1}. The chamber
229   block temperature was controlled to minimize variation in leaf temperature and was set at 30.1 $\pm$ 0.9°C.
230   Pre-treatment measurements of the mature trees were carried out in both wet (May-June) and dry season (October-November)
231   of 2015, except for the wet season measurements of the plots at Paracou situated at the slope which were measured in June
232   2016 due to practical constraints. After three years of nutrient addition, we repeated the leaf gas exchange measurements of
233   the mature trees in the wet season (May-June) of 2019. We measured leaf gas exchange of leaves collected at two different
234   canopy heights, estimated relative to the top of the canopy: sunlit, upper canopy foliage and shaded, lower canopy foliage.
235   Branch excision prior to measuring leaf gas exchange was necessary to reach the canopy leaves. The excised branches (ca.
236   2 m-long) were cut by a tree climber and immediately recut under water to restore hydraulic conductivity (Domingues et al.,
237   2010; Dusenge et al., 2015; Rowland et al., 2015; Verryckt et al., 2020b). Photosynthesis measurements of the saplings were
238   carried out on leaves still attached to the trees and were performed in August 2016 (pre-treatment) and August 2017 (1-year
239   of nutrient addition). All photosynthesis measurements were conducted between 09:00 and 16:00 (local time).

240   **4.2.1 Photosynthetic CO_2-response curves**

241   Photosynthetic CO_2-response curves (Figure 4) were established by measuring net photosynthetic rates (A_n) at different CO_2
242   concentrations by controlling the reference CO_2 concentrations, while maintaining a constant temperature and photosynthetic
243   photon flux density (PPFD). The A_n-C_i (Ci, the CO_2 concentration of the leaf intercellular spaces) measurements began at the
244   ambient CO_2 concentration of 400 ppm. Once a steady state of photosynthesis was reached, the CO_2 concentrations was
245   reduced stepwise to 50 ppm, then returned to 400 ppm, and thereafter increased to 2000 ppm, to obtain a total of 10-14
246   measurements per leaf. We measured A_n-C_i curves for one to three leaves per canopy level, resulting in a total of 1708 curves
247   measured (Table 3). The methods used here are described in protocol 2.1.3 Leaf-scale photosynthesis in the Supporting

248 Information S2 Carbon and nutrient cycling in Halbritter et al. (2020). Additionally, we measured leaf dark respiration (R_d) by

249 taking five consecutive measurements on one leaf per branch level, after keeping the branch in complete darkness for 30 min.

250 The A_n-C_i curves were carried out at a saturating PPFD level of 500 and 1300µmol m^{-2} s^{-1} for shaded, lower canopy and sunlit,

251 upper canopy leaves, respectively. Verryckt et al. (2020a) showed that 500 µmol m^{-2} s^{-1} is below light-saturation and a PPFD

252 level of 800 µmol m^{-2} s^{-1} would have been optimal for shaded, lower canopy leaves. Increasing the PPFD level would, however,

253 only result in a small increase of net photosynthesis.

254 The A_n-C_i curves present A_n at any given C_i as the minimum of three potential limitations: rubisco (V_{cmax}), ribulose 1,5-

255 biphosphate (J_{max}) or triose phosphate use (TPU). These curves were fitted with the FvCB model using the fitaci function from

256 the "Plantecophys" package (Duursma, 2015) in R 3.3.3 (R Core Team, 2019) to obtain the biochemical parameters V_{cmax}, J_{max}

257 and, when possible, TPU.

258 **4.2.2 Light-saturated photosynthesis (A_{sat}) of saplings**

259 Light-saturated photosynthesis (A_{sat}) and the stomatal conductance (g_s) were measured, separately from the A_n-C_i curves, for

260 the saplings at the Paracou plots situated at the bottom valleys and hilltops. We used the methods described in protocol 2.1.3

261 Leaf-scale photosynthesis and protocol 5.7 Stomatal conductance in the Supporting Information, respectively, S2 Carbon and

262 nutrient cycling and S5 Stress physiology in Halbritter et al. (2020). The CO_2 concentration was maintained at 400 ppm and a

263 the PPFD was set at 500 µmol m^{-2} s^{-1}. In 2016, A_{sat} and g_s were measured on one leaf per individual and for three to five

264 individuals per species. This resulted in a total of 159 measurements. In 2017, after 1-year of nutrient addition, these

265 measurements were repeated on the same individuals when they survived, and on additional saplings resulting in 195

266 measurements in total.

267 **4.3 Leaf traits**

268 All leaves used for gas exchange were collected and, for the mature trees, leaf chlorophyll was estimated by averaging five

269 chlorophyll content measurements from each leaf with a CCM-200 portable chlorophyll meter (Opti-Sciences, Tyngsborough,

270 MA, USA), thereby avoiding major veins and areas of obvious visual damage or disease. A unitless chlorophyll content index

271 (CCI) value was calculated from the ratio of optical absorbance at 655 nm to that at 940 nm. Then, the leaves were scanned to

272 obtain the leaf area, dried for at least 48 h and weighed. Leaf area was measured with the leaf area meter LI-3100C (LI-COR,

273 Lincoln, NE, USA), which, together with the leaf dry mass, was used to calculate the specific leaf area (SLA). After grinding

274 the dried leaves, leaf nutrient concentrations were determined in accordance with protocol 2.1.6 Foliar nutrient stoichiometry

275 and resorption in Supporting information S2 Carbon and nutrient cycling in Halbritter et al. (2020). Leaf C and N

276 concentrations of 10 mg subsamples were determined by dry combustion using a Flash 2000 elemental analyzer (Thermo

277 Fisher Scientific, Germany). Leaf P concentration of 0.1 g subsamples was determined by an acid digestion method (Walinga

278 et al., 1989) on a Skalar SAN++ continuous flow analyzer, and thereafter analyzed on an iCAP 7400 radial optical emission

9

279 spectrometer (Thermo Fisher Scientific, Germany) to determine the concentration of leaf K, Ca, Mg, and Mn. Samples were

280 ashed, digested with nitric acid (HNO_3) and filtered prior to analysis.

281 In the wet season of 2015, we also analyzed leaf S, Na, V, Sr, As, Cd, Cr, Cu, Fe, Pb, Zn and Mo on a model 7500ce ICP-MS

282 spectrometer (Agilent Technologies, Tokyo, Japan) after digestion with HNO_3.

283 For saplings, total phenolic concentration of the leaves was measured using an improved Folin-Ciolcalteu assay (Singleton

284 and Rossi, 1965; Marigo, 1973) and total leaf tannin concentration of the leaves was determined with the butanol/HCl method

285 (Porter et al., 1985) modified as in Makkar and Goodchild (1996). The extracts for both phenol and tannin concentrations were

286 determined using a Helios Alpha spectrophotometer (Thermo Spectronic, Cambridge, UK) at 760 and 550 nm, respectively.

287 Both methods are described in detail in Peñuelas et al. (2010).

288 **4.4 Ancillary data**

289 The vertical structure of a tropical rainforest is complex and multi-layered, resulting in great variation in light availability

290 within the canopy (Yoda, 1974). We assessed the light environment of each studied tree by visually estimating the canopy

291 light exposure or Dawkins' crown illumination index (Dawkins, 1958). This index describes a tree's light environment based

292 on a five-point scale ranging from (1) no direct light for suppressed trees to (5) crown fully illuminated for emergent trees

293 (Figure 5).

294 Sampling height of the mature trees was measured with a Forestry Pro rangefinder (Nikon, Tokyo, Japan) by tree climbers

295 situated at sampling height pointing towards the soil. For saplings, we measured the total height of the tree using a measuring

296 tape, and additionally we measured the diameter at 10 cm and at 50 cm above surface level. On top of each sapling, we

297 measured leaf area index (LAI) with the LAI-2000 (LI-COR, Lincoln, NE, USA) during periods of overcast sky.

298 Herbivory rates, i.e. foliar damage by herbivores, of the saplings was estimated as punctual herbivory (%) according to Pirk

299 and Farji-Brener (2012). We visually assessed the missing area of the leaf and assigned each leaf to the following categories:

300 0, 0.1-5, 5.1-25, 25.1-50, 50.1-100 % area consumed. We calculated the percentage of foliar damage per sapling by multiplying

301 the number of leaves of each category by the mid-point foliar damage of each category (i.e. 0, 2.5, 15, 37.5, 75 % respectively)

302 and dividing this result by the total number of leaves per sapling. To test the accuracy of this method, we photographed 106

303 leaves we visually assessed and compared visual estimations of herbivory in the field using ImageJ. In 90% of the cases

304 categories were well assigned.

305 **5 V_{cmax} of sunlit, upper canopy leaves**

306 TBMs use plant functional types (PFT) to represent broad groupings of plant species that share similar characteristics (e.g.

307 growth form) and roles (e.g. photosynthetic pathway) in ecosystem function (Rogers et al., 2017). Although all TBMs share

308 this approach, they differ from each other in how narrow or broad the PFTs are defined. Depending on the TBM, tropical

309 rainforests belong to "broadleaf evergreen tropical tree", "tropical tree", "rainforest", "evergreen broadleaf tree" or "broadleaf

310 tree" (Figure 6A). Although our mean values of photosynthetic capacity of sunlit, upper canopy leaves are in line with those
311 of other tropical rainforest sites (Figure 6B), many TBMs use estimates for V_{cmax} that are much higher than the estimates from
312 leaf-level measurements (Figure 6A). Only three TBMs (Orchidee, O-CN, and Bethy), which have adopted detailed PFTs, are
313 within the range of our measurements. Some TBMs might obtain more accurate estimates of the global C budget by dividing
314 the adopted PFTs into more detailed PFTs. Hybrid, for example, uses the classification "rainforest", which includes both
315 temperate and tropical rainforest, leading to much higher V_{cmax} values. This is also true for the PFT "evergreen broadleaf tree"
316 used in CTEM and BIOME-BGC, and the PFT "broadleaf tree" used in "JULES".
317

318 ## 6 Challenges of fieldwork in the tropics

319 Fieldwork in the tropical rainforest is challenging because of its remoteness and extremely moist and warm climate. While
320 Paracou is only a 45 min-drive from a major city, Kourou, Nouragues can only be reached by helicopter (30 min from Cayenne,
321 the capital of French Guiana) or a combination of car (2 h from Cayenne) and motorized canoe (4-6 h from Regina to
322 Nouragues). Carrying out fieldwork in such a remote location requires adequate logistical planning and funding, as both people
323 and material need to be transported to this remote site and stay there for prolonged periods. Proper planning and coordination
324 with the whole team was required to get the fieldwork finished within a limited timeframe.
325 The combination of high temperature and humidity poses an additional hurdle as this generally makes physical exertion harder
326 than in temperate climates and, most importantly, decreases the longevity of most if not all electronic devices. Indeed, we
327 suffered from several Li-6400XT malfunctions, as well as defects of laptops, freezers and drying ovens. However, these defects
328 did not reduce the reliability of our data, but it required extra precautions and increased expenses. We tested, for example, the
329 Li-6400XT devices each morning and the devices were regularly cross-calibrated. Malfunctions of these devices led to
330 troubleshooting and extra testing before new measurements were carried out, which can be very time consuming and did have
331 an impact on the amount of data that could be gathered. Laptops and other electronic devices were best stored overnight in a
332 waterproof bag/barrel, whereas regularly moving them in and out of air-conditioned rooms increased malfunctions.
333 Additionally, access to power was limited and a portable generator was often required to carry out all photosynthesis
334 measurements.
335 The tropical soil is hard, making it very labour intensive to take soil cores and posing several other problems. Soil corers
336 deformed as they are not developed for tropical soil types and the installation of PRS probes without breaking them was very
337 challenging. Another challenge is reaching upper canopy leaves up to > 50 m height above ground level, which required
338 technical tree climbing skills and equipment from experienced tree climbers.
339 High species diversity and stand structural complexity of tropical forests are a major challenge to understand the ecosystem
340 functioning of tropical forests and force researchers to study either some abundant species following them in time or to take
341 into account the high diversity limiting the number of replicates per species.

342 **76 Data availability**

343 This Photosynthesis-Soil database is provided as an excel workbook and is freely available at DOI
344 10.5281/zenodo.5638236~~10.5281/zenodo.4719242~~. Photosynthetic CO_2-response curves are presented as raw A_n-C_i files
345 which can be analyzed by any user of the database, but V_{cmax} and J_{max} values, fitted using the "Plantecophys" package
346 (Duursma, 2015) in R, can also be found in the database in addition to the leaf traits. The soil database of 2015, including bulk
347 density, soil particle size distribution, soil moisture and nutrients, and the fertilizer composition are shown in separate sheets.

348 **87 Summary**

349 Publicly accessible and usable datasets from experimental sites are needed to greatly enhance the power of data synthesis as
350 well as model development and evaluation (Vicca et al., 2018; Halbritter et al., 2020). We provide vertical profiles of
351 photosynthetic capacity data and important leaf traits from two three-year large-scale nutrient addition experiments conducted
352 in two tropical rainforests in French Guiana. Our dataset is extremely valuable to the modelling and tropical ecology
353 community as we present a valuable source of information to further improve model representations of the roles of leaf
354 nutrients in photosynthesis in tropical forests. We present raw A_n-C_i curves, which allows the curves to be fit under the same
355 assumptions as curves collected at other sites, avoiding bias in the method of analysis. In addition, we provide V_{cmax} and J_{max}
356 values making these values immediately available to the modelling community. We provide leaf-level photosynthesis data at
357 several heights within the canopy from mature trees and saplings allowing to study differences in sunlit and shaded leaves.
358 Ancillary data such as herbivory and leaf phenol concentration can be of great value as additional data to other studies on these
359 topics. A large set of soil properties and nutrient availabilities in the soils underlying the studied trees were made available as
360 these data are highly relevant to understand how and why nutrient availability interacts with C uptake in tropical forests.

361 **Author contribution**

362 L.T.V., L.V.L., C.S., D.A., I.U., R.O., J.L., O.G., G.P., A.G.G., E.A.C., O.M., P.C., M.O., L.F., L.L., , P.R.F.G., H.V., M.V.,
363 C.R., and I.A.J. contributed to the field work and collected the data. P.R.F.G., M.P.E. and P.V. carried out the majority of the
364 lab analysis. The manuscript was drafted by L.T.V., I.A.J. and S.V. and was further revised by all co-authors.

365 **Competing interests**

366 The authors declare that they have no conflict of interest.

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539 **Tables**

540 **Table 1 Surface soil (0-15 cm) total and available nutrient concentrations measured in 2015 in the three landscape positions**
541 **(topography; B = bottom, S = slope, T = top) and separated by season. Standard errors are shown (n = 20).**

Site	Season	Topography	C	N	P	$NO_3^- + NH_4^+$ (1M KCl extraction)	Bray P
			(%)	(%)	(%)	(ppm)	(ppm)
Paracou	wet	B	1.7 +- 0.1	0.13 +- 0.01	81 +- 4	9.6 +- 1.1	3.3 +- 0.3
		S	2.3 +- 0.2	0.16 +- 0.01	117 +- 9	25.6 +- 3.0	1.3 +- 0.1
		T	1.9 +- 0.1	0.14 +- 0.01	76 +- 9	15.3 +- 1.7	1.3 +- 0.1
	dry	B	2.5 +- 0.2	0.17 +- 0.01	89 +- 6	4.6 +- 0.4	2.8 +- 0.2
		S	2.6 +- 0.2	0.18 +- 0.01	139 +- 10	11.6 +- 0.9	0.9 +- 0.3
		T	2.1 +- 0.1	0.14 +- 0.01	75 +- 4	5.9 +- 0.3	1.2 +- 0.1
Nouragues	wet	B	2.5 +- 0.2	0.19 +- 0.02	56 +- 5	9.3 +- 0.8	1.7 +- 0.2
		S	2.7 +- 0.1	0.20 +- 0.01	84 +- 3	7.7 +- 0.5	0.9 +- 0.1
		T	4.2 +- 0.2	0.30 +- 0.01	311 +- 20	16.4 +- 1.0	0.9 +- 0.1
	dry	B	3.1 +- 0.2	0.22 +- 0.01	67 +- 5	9.0 +- 0.9	2.1 +- 0.1
		S	3.5 +- 0.2	0.24 +- 0.01	91 +- 4	11.2 +- 1.0	1.2 +- 0.1
		T	4.5 +- 0.2	0.30 +- 0.01	308 +- 21	15.0 +- 0.8	1.3 +- 0.1

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546 **Table 2 Overview of the amount of mature trees and species measured in each plot at Nouragues-Inselberg (NOU-I), Nouragues-**
547 **Pararé (NOU-P) and Paracou (PAR). Values between brackets indicate the amount of different species measured per plot, in case**
548 **this differe**

		2015		2016	2017	2019
		DRY	WET	WET	DRY	WET
NOU-I	B1	3	5			5
	B2	2	3			2
	B3	4	3			4
	B4	5	5			5
	S1	4	3			4 (3)
	S2	3	5 (4)			5 (4)
	S3	4	5 (4)			5 (4)
	S4	3	5			5
	T1	4	5			5
	T2	4	5			5
	T3	3	5			5
	T4	3	5			5
NOU-P	COPAS				12 (9)	
PAR	B1	5	5			5
	B2	5	5			5
	B3	5	5			4
	B4	5 (4)	5 (4)			5 (4)
	S1	5		5		5
	S2	5 (4)		4 (3)		5 (4)
	S3	4		4		5
	S4	4		3		5 (4)
	T1	4	5 (4)			5 (4)
	T2	5 (3)	4 (3)			4 (3)
	T3	5	4			5
	T4	4	4			5

549

550 **Table 3 Overview of the number of A_n-C_i curves measured in this study. Measurements were carried out in the wet and dry season,**
551 **at different canopy levels (U = upper canopy, sunlit leaves; L = lower canopy, shaded leaves; M = middle canopy leaves), at different**

	Nouragues-Inselberg				Nouragues-Pararé			Paracou				Paracou-Saplings
	U		L		U	M	L	U		L		
	wet	dry	wet	dry	dry	dry	dry	wet	dry	wet	dry	
2015	141	82	146	76				61	113	56	120	
2016								42		35		38
2017					37	45	32					46
2019	156		163					155		164		

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556 **Figures**
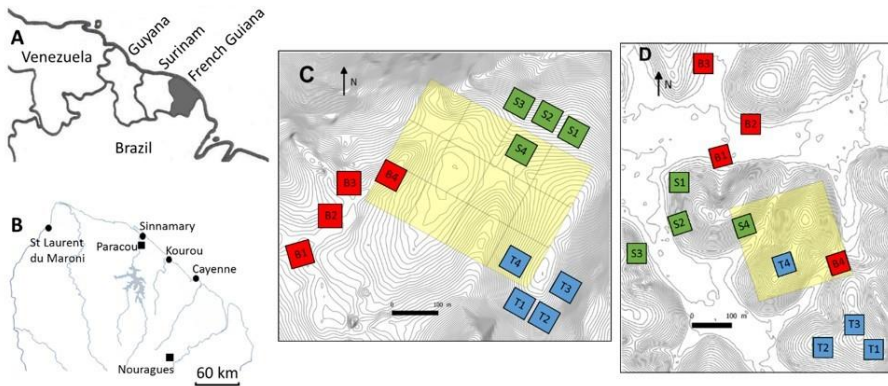
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558 **Figure 1 Situational map: (A) north-eastern part of South America, (B) northern French Guiana with its main cities (circles) and**
559 **the experimental sites Paracou and Nouragues (closed squares), (C) the twelve study 50 x 50 m plots of this study at Nouragues-**
560 **Inselberg, (D) the twelve study 50 x 50 m plots of this study at Paracou. Adapted from Ferry et al. (2010) and Courtois et al. (2018).**
561 **Plots are marked by a letter describing the topography (B = bottom, S = slope, T = top) and a number describing the nutrient**
562 **addition treatment (1 = +N, 2 = +NP, 3 = +P, 4 = control).**
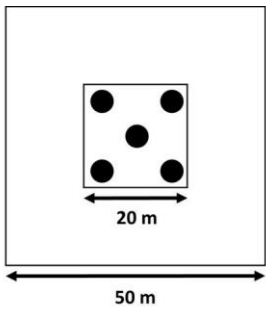
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564 **Figure 2 Soil sampling design according to a 5-on-dice pattern, performed in the central 20 x 20 m area within each of the 50 x 50 m**
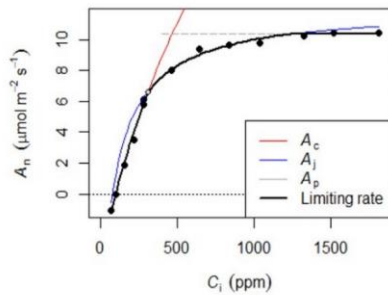
565 **plots.**
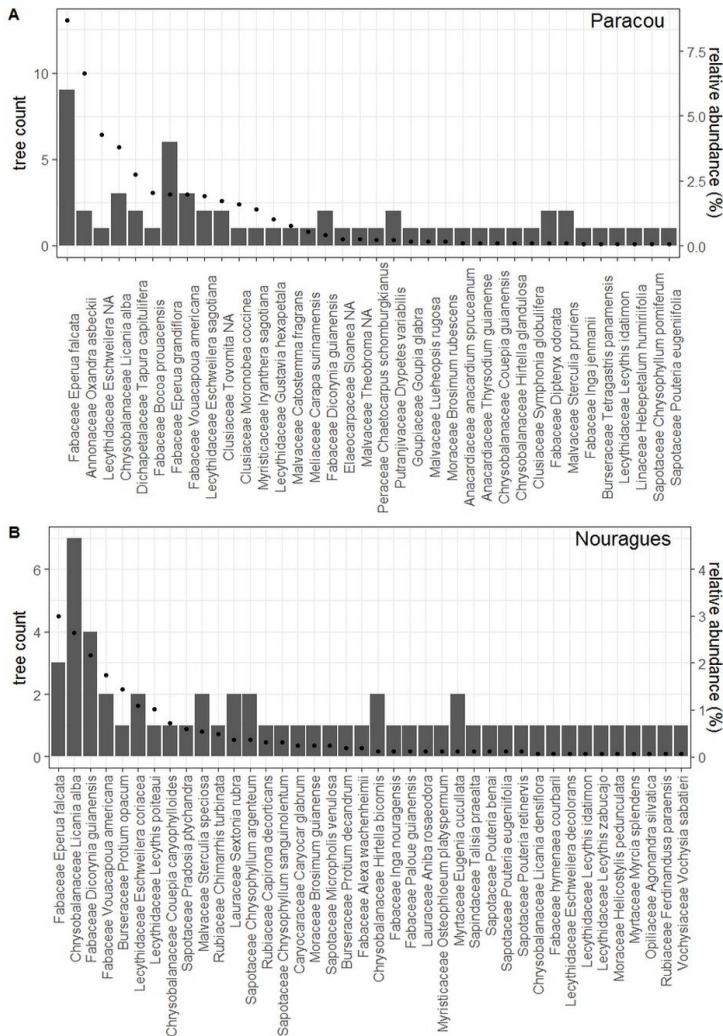
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567 **Figure 3 Number of mature trees we sampled per species (bars) and the relative abundance for each species (dots) are shown for (A)**
568 **Paracou and (B) Nouragues. Relative abundance was calculated as the percent composition of each species relative to the total**
569 **number of that species with all 50 x 50 m plots at Paracou or Nouragues.**

570

Figure 4 Example of the A_n-C_i response. Net photosynthesis (A_n) at any given C_i is the minimum of three potential limitations:

rubisco (A_c), RuBp (A_j) or TPU (A_p).

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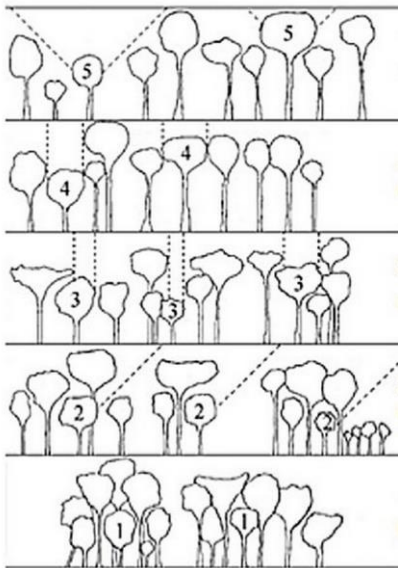
Figure 5 Classification of the Dawkins' crown illumination index (adapted from Dawkins 1958): (1) no direct light, (2) low lateral

light, (3) some vertical light (10-90% of the vertical projection of the crown exposed to vertical illumination), (4) crown completely

exposed to vertical light, but lateral light blocked within some or all of the 90° inverted cone encompassing the crown (5) crown fully

exposed to vertical and lateral illumination.

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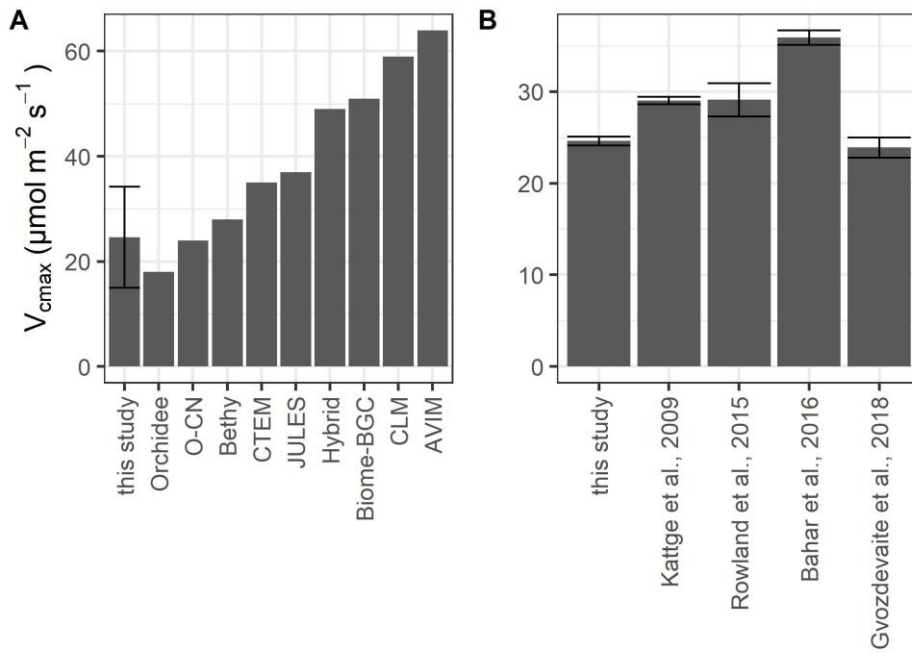
Figure 6 *Values of V_{cmax} at 25∘C for sunlit, upper canopy leaves measured in this study compared to (A) different model estimates and (B) other lowland tropical sites growing on nutrient-poor oxisols. The values for the models were adopted from Rogers (2014) for the plant functional types "broadleaf evergreen tropical tree" (Orchidee, O-CN, CLM, AVIM), "tropical tree (oxisol)" (Bethy), "rainforest" (Hybrid), "evergreen broadleaf tree" (Biome-BGC, CTEM), and "broadleaf tree" (Jules). We did not include IBIS, which was also mentioned in Rogers (2014), as the source of the data is unclear. Error bars in (A) show the standard deviation and in (B) the standard error.*

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