



# 1 Vertical profiles of leaf photosynthesis and leaf traits, and soil 2 nutrients in two tropical rainforests in French Guiana before and 3 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.4719242 (Verryckt, 2021).

## 47 **1 Introduction**

48 Tropical forests play a significant role in the global carbon (C) cycle, contributing more than one third of global terrestrial  
49 gross primary productivity (GPP) (Beer et al., 2010; Malhi, 2010). To obtain accurate estimations of the global C budgets, a  
50 thorough understanding of the functioning of these tropical forests is thus important. It is still highly uncertain how these  
51 tropical forests, and in particular lowland tropical forests, respond to nutrient limitation and to global change in terms of C  
52 uptake (Fleischer et al., 2019; Wieder et al., 2015).

53 Leaf photosynthetic capacity is the primary driver of C uptake and its accurate representation in terrestrial biosphere models  
54 (TBMs) is essential for robust projections of C stocks and fluxes under global change scenarios. Photosynthesis in  $C_3$  species  
55 is typically represented in nearly every major large-scale TBM by the Farquhar, von Caemmerer and Berry (FvCB) model of  
56 photosynthesis (Farquhar et al., 1980; von Caemmerer and Farquhar, 1981).

57 The FvCB model determines photosynthesis ( $A$ ) by the most limiting of two processes, Rubisco activity and electron transport.  
58 Empirical studies to determine the key parameters of these two processes (i.e. the maximum rate of carboxylation  $V_{cmax}$ , the  
59 maximum electron transport rate,  $J_{max}$ ) and to test empirically their limitations on the leaf- and canopy-scale are necessary for  
60 obtaining the data required for parameterizing the FvCB model (Medlyn et al., 2015). Plant trait databases, now widely  
61 available, offer an excellent opportunity for parameterizing models. However, data on tropical forests are sparse and highly  
62 variable due to the huge species diversity (Rogers, 2014).

63 Moreover, empirical studies on leaf photosynthesis and leaf traits in tropical forests have mainly focused on upper canopy  
64 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  
65 species in these highly diverse tropical forests. Subsequently, light and leaf nitrogen (N) profiles are used to upscale leaf- to



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

71 Environmental drivers are key to improve our understanding of C-nutrient cycle interactions and our ability to model them.  
72 Climate data are often directly available at high spatial resolution and at the global scale from databases such as Worldclim  
73 (Ruiz-Benito et al., 2020), while observations of soil properties and soil nutrient availability are often missing (Vicca et al.,  
74 2018). Soil variables have been shown to be strong predictors of leaf traits in higher plants (Maire et al., 2015). Comprehensive  
75 soil data, including soil properties such as texture and pH as well as important nutrients, are needed to further enhance our  
76 understanding of how and why nutrient availability interacts with C uptake in tropical ecosystems and their responses to global  
77 environmental change (Vicca et al., 2018).

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

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

## 88 **2 Sampling sites**

### 89 **2.1 Study site description**

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

96 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  
97 average annual rainfall of 3100 mm year<sup>-1</sup> (2004 – 2015) (Aguilos et al., 2019). The average density of trees with a diameter



98 at breast height (DBH) > 10 cm is ca. 620 trees ha<sup>-1</sup>, and tree species richness averaged ca. 160 species ha<sup>-1</sup> (Bonal et al., 2008).  
99 The mean canopy height was 35 m, with emergent trees exceeding 40 m. The second study site, the Nouragues Research  
100 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  
101 Inselberg station (Petit Plateau) and near the Pararé station (COPAS). The Nouragues forest receives approximately  
102 3000 mm rain year<sup>-1</sup> and tree density (DBH > 10 cm) averaged ca. 535 trees ha<sup>-1</sup> (Bongers et al., 2001). Tree species richness  
103 ranges between 180 and 200 species ha<sup>-1</sup>. The canopy height varies between 30 and 40 m, with emergent trees reaching 60 m  
104 (Van Der Meer et al., 1998).

105 The soils at Paracou are derived from the Bonidoro series, characterized by schist and sandstones and locally crossed by veins  
106 of pegmatite, aplite and quarsites (Gourlet-Fleury et al., 2004; Epron et al., 2006), whereas the soils of Nouragues have a  
107 weathered granite parent material of the Caraibe series (van der Meer and Bongers, 1996; Bongers et al., 2001). According to  
108 the USDA texture classification chart, the soils at Paracou range from loamy sand to sandy loam and at Nouragues from sandy  
109 loam to silty clay (Van Langenhove et al., 2019). These old and highly weathered soils at both sites are characterized as  
110 nutrient-poor Acrisols (FAO, 1998) and are, compared to the generally younger, nutrient-rich soils of western Amazonia,  
111 particularly low in P concentration (Hammond, 2005; Grau et al., 2017).

112 At both forest sites, an instrumentation tower is in place at which meteorological measurements and measurements of  
113 ecosystem net CO<sub>2</sub> exchange with the eddy covariance technique have been carried out on a continuous basis since 2003 in  
114 Paracou (Bonal et al., 2008) and since 2014 at Nouragues.

## 115 **2.2 Nutrient addition experiment**

### 116 **2.2.1 Set-up**

117 In 2015, we set up twelve 50 x 50 m plots, in three blocks of four plots, along a toposequence at Paracou and Nouragues,  
118 resulting in a total of 24 plots. These blocks were located at distinct landscapes: (1) bottom, i.e. just above the creek running  
119 through the valley, (2) slope, i.e. the intermediate section of the elevation and (3) top, i.e. where the slope evens out and  
120 becomes the hilltop (Courtois et al., 2018). The valley bottoms and hilltops differ ca. 20–50 m in elevation over horizontal  
121 distances of 200–400 m (Van Langenhove et al., 2019), with maximum altitudes of ca. 70 m and 120 m for Paracou and  
122 Nouragues, respectively (Courtois et al., 2018).

123 In October 2016, a field nutrient addition experiment at both sites was initiated and is ongoing to this day. In each block, one  
124 plot served as control plot and the remaining three plots received one of three nutrient addition treatments (+N, +P or +NP).  
125 Fertilizer was applied twice per year by hand-broadcasting commercial urea ((NH<sub>2</sub>)<sub>2</sub>CO) and/or triple superphosphate  
126 (Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>) at a rate of 125 kg N ha<sup>-1</sup> y<sup>-1</sup> (+N treatment) or 50 kg P ha<sup>-1</sup> y<sup>-1</sup> (+P treatment), or both amounts together (+NP  
127 treatment). These application rates are identical as those in the ongoing nutrient addition experiment in Barro Colorado Nature  
128 Monument in Panama, which was initiated in 1998 (Wright et al., 2011), and the Amazon Fertilization Experiment (AFEX)  
129 near Manaus in Brazil, initiated in 2017 (Lugli et al., 2021), to enable future comparison of our results. In Paracou, these rates



130 of nutrient addition represent, respectively, 130% and 250% of yearly N and P input through litterfall and atmospheric  
131 deposition combined (Van Langenhove et al., 2020b).

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

### 135 **2.2.2 Fertilizer composition**

136 Within the nutrient addition experiment, N was added as commercial urea ((NH<sub>2</sub>)<sub>2</sub>CO) and P as triple superphosphate  
137 (Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>). The chemical composition of the applied fertilizers was analyzed to know the exact composition. Samples of  
138 both fertilizers were dried at 70°C for 48 h, after which they were ground. Total N of the fertilizers was determined by dry  
139 combustion using a Skalar Primacs (Skalar Holding, The Netherlands). P<sub>2</sub>O<sub>5</sub> and MgO in mineral acid were determined by  
140 an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany). The ground samples were analyzed  
141 with an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany) to determine the potassium (K),  
142 calcium (Ca) and magnesium (Mg) concentrations, as well as the heavy metal concentrations (arsenic (As), cadmium (Cd),  
143 chromium (Cr), copper (Cu), iron (Fe), nickel (Ni), lead (Pb), zinc (Zn), molybdenum (Mo)).

## 144 **3 Data and Methods: soil sampling**

### 145 **3.1 Sampling design**

146 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  
147 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  
148 cylindrical head (8-cm diameter). Additionally, we took three soil cores with a gouge auger (30-cm length, 5-cm diameter).  
149 These three cores were split into two depths (0-15 cm and 15-30 cm), pooled together per depth and used for gravimetric soil  
150 water content determination, soil particle size distribution analysis and chemical analysis after sieving (< 2 mm). We divided  
151 the soil into a ‘surface’ layer (0–15 cm) and a ‘deeper’ layer (15–30 cm) instead of sampling by generic horizon because the  
152 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  
153 beyond (Van Langenhove et al., 2020c; Guitet et al., 2016; Bongers et al., 2001). In 2019, after 3 years of nutrient addition,  
154 the soil sampling was repeated. However, these data have not been processed yet and will be made available through  
155 publication as soon as possible.



## 156 **3.2 Soil physical properties**

### 157 **3.2.1 Bulk density**

158 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  
159 sieved through a 2-mm sieve. We collected the soil fraction, the roots and the stones, which were dried and weighed separately  
160 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  
161 soil core divided by its volume (i.e. the volume of the auger, 754 cm<sup>3</sup>), whereas exclusive bulk density is calculated by dividing  
162 the total weight of the soil fraction (excluding roots and stones) by the volume of the entire core (i.e. 754 cm<sup>3</sup>).

### 163 **3.2.1 Soil particle size distribution**

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

### 171 **3.2.3 Soil moisture**

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

## 175 **3.3 Soil nutrients**

### 176 **3.3.1 Chemical analyses: concentrations and availability**

177 Freshly sieved soil was used for the measurement of pH and the extraction of inorganic N (N<sub>i</sub>) and inorganic P (P<sub>i</sub>). We  
178 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  
179 ratio and shaking it for 1 h. The same solution was passed through a 42-µm filter and the filtrate's concentration of NH<sub>4</sub><sup>+</sup> and  
180 NO<sub>3</sub><sup>-</sup> was determined colourimetrically (SAN++ continuous flow analyzer, Skalar Inc., The Netherlands). The P<sub>i</sub> was extracted  
181 with the Olsen-P bicarbonate extraction (Olsen et al., 1954) and measured on an iCAP 6300 Duo ICP optical emission  
182 spectrometer (Thermo Fisher Scientific, Germany).

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



185 by analysis on an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany). Water soluble  
186 molybdate ( $\text{MoO}_4^{2-}$ ) and phosphate ( $\text{PO}_4^{3-}$ ) were determined through resin extraction on previously dried ( $60^\circ\text{C}$ ) soil  
187 (Wurzburger et al., 2012). The soil samples were mixed with water in a 1:6 ratio and five 2-cm<sup>2</sup> strips of anion-exchange  
188 membrane (VWR Chemicals, USA) were added (Van Langenhove et al., 2019; Wurzburger et al., 2012). After stirring this  
189 mixture 24 h, the strips were rinsed and eluted with 10%  $\text{HNO}_3$ . The concentrations of water soluble  $\text{MoO}_4^{2-}$  and  $\text{PO}_4^{3-}$  were  
190 analyzed with an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany).

191 Additionally, we analyzed total macro- and micronutrient concentrations on previously dried soil. Soil C and N concentrations  
192 were determined by dry combustion with a Flash 2000 elemental analyzer (Thermo Fisher Scientific, Germany), and total soil  
193 C and N was analyzed by EA-IRMS (EA1110, CE Instruments, Milan, Italy), coupled to a Finnigan MAT Delta Plus IRMS  
194 (Thermo Fisher Scientific, Germany). The concentrations of P, K, Ca, Mg, sulphur (S), manganese (Mn), sodium (Na),  
195 vanadium (V), strontium (Sr), As, Cd, Cr, Cu, Fe, Ni, Pb, Zn and Mo were obtained by acid digestion in an ultraWAVE  
196 digester (Milestone, Italy), followed by ICP-MS (7500ce model, Agilent Technologies, Tokyo, Japan) analysis.

### 197 3.3.2 PRS probes

198 We used Plant Root Simulator (PRS ®) probes (Western Ag Enterprises, Inc., Saskatoon, CA) to provide proxies for plant  
199 available ions in soil solution (Van Langenhove et al., 2020a; Halbritter et al., 2020). These PRS probes are ion exchange resin  
200 membranes (IEM; approximately 5.5 cm × 1.6 cm, or 17.5 cm<sup>2</sup> including both sides of the IEM) held in plastic supports that  
201 were vertically inserted into soil with minimal disturbance (Hangs et al., 2004). In each plot, we installed five root exclusion  
202 cylinders (REC) following a five-on-a-dice design to study soil nutrient dynamics in absence of the root system (Van  
203 Langenhove et al., 2020a). RECs were PVC collars inserted 20 cm into the soil to sever all near-surface roots and mycorrhizal  
204 fungal hyphae, and were installed prior to the first soil nutrient measurements in May 2015.

205 In both the wet (May) and dry (October) season of 2015, we installed four anion and four cation probes, which formed one  
206 sample, into each REC. After a period of two weeks, the PRS<sup>TM</sup> probes were removed from the soil, washed with distilled  
207 water and shipped to the manufacturer for analysis of the following nutrients: P, K, Ca, Mg, S, Mn, Cd, Cu, Fe, Pb, Zn, nitrate  
208 ( $\text{NO}_3$ ), ammonium ( $\text{NH}_4$ ), boron (B) and aluminium (Al). In situ burial of the PRS<sup>TM</sup> probes provide a dynamic measure of  
209 nutrient flux, or nutrient supply rate to an ion sink (Gibson et al., 1985; Casals et al., 1995). The results are thus expressed as  
210 the amount of nutrient adsorbed per surface area of IEM during the duration of burial (Qian and Schoenau, 2002). In our study  
211 it was expressed as  $\mu\text{g}$  nutrient 10 cm<sup>-2</sup>.for two weeks.

## 212 4 Data and Methods: leaf sampling

### 213 4.1 Tree selection

214 In each 20 x 20 m plot at Paracou and Nouragues, we selected five mature trees, of which three were top-canopy species likely  
215 dominating the functioning of the plot and two trees were sub-canopy species. Additionally, we selected twelve trees at the



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

## 220 **4.2 Photosynthesis**

### 221 **4.2.1 Leaf gas exchange**

222 We measured leaf gas exchange measurements using a set of infrared gas analyzers (IRGAs) incorporated into a portable  
223 photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, USA). A leaf was clamped within a chamber with controlled  
224 microenvironmental conditions during the measurements and the device measures the concentration changes of water vapour  
225 ( $H_2O$ ) and carbon dioxide ( $CO_2$ ) between incoming and outgoing air. The relative humidity inside the chamber ( $67.9\% \pm 0.06$ )  
226 was kept as close to ambient as possible during the measurements and the air flow rate was set at  $500 \mu\text{mol s}^{-1}$ . The chamber  
227 block temperature was controlled to minimize variation in leaf temperature and was set at  $30.1 \pm 0.9^\circ\text{C}$ .

228 Pre-treatment measurements of the mature trees were carried out in both wet (May-June) and dry season (October-November)  
229 of 2015, except for the wet season measurements of the plots at Paracou situated at the slope which were measured in June  
230 2016 due to practical constraints. After three years of nutrient addition, we repeated the leaf gas exchange measurements of  
231 the mature trees in the wet season (May-June) of 2019. We measured leaf gas exchange of leaves collected at two different  
232 canopy heights, estimated relative to the top of the canopy: sunlit, upper canopy foliage and shaded, lower canopy foliage.

233 Branch excision prior to measuring leaf gas exchange was necessary to reach the canopy leaves. The excised branches (ca.  
234 2 m-long) were cut by a tree climber and immediately recut under water to restore hydraulic conductivity (Domingues et al.,  
235 2010; Dusenge et al., 2015; Rowland et al., 2015; Verryckt et al., 2020b). Photosynthesis measurements of the saplings were  
236 carried out on leaves still attached to the trees and were performed in August 2016 (pre-treatment) and August 2017 (1-year  
237 of nutrient addition). All photosynthesis measurements were conducted between 09:00 and 16:00 (local time).

### 238 **4.2.1 Photosynthetic $CO_2$ -response curves**

239 Photosynthetic  $CO_2$ -response curves (Figure 4) were established by measuring net photosynthetic rates ( $A_n$ ) at different  $CO_2$   
240 concentrations by controlling the reference  $CO_2$  concentrations, while maintaining a constant temperature and photosynthetic  
241 photon flux density (PPFD). The  $A_n-C_i$  ( $C_i$ , the  $CO_2$  concentration of the leaf intercellular spaces) measurements began at the  
242 ambient  $CO_2$  concentration of 400 ppm. Once a steady state of photosynthesis was reached, the  $CO_2$  concentrations was  
243 reduced stepwise to 50 ppm, then returned to 400 ppm, and thereafter increased to 2000 ppm, to obtain a total of 10-14  
244 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  
245 measured (Table 1). The methods used here are described in protocol 2.1.3 Leaf-scale photosynthesis in the Supporting





246 Information S2 Carbon and nutrient cycling in Halbritter et al. (2020). Additionally, we measured leaf dark respiration ( $R_d$ ) by  
247 taking five consecutive measurements on one leaf per branch level, after keeping the branch in complete darkness for 30 min.  
248 The  $A_n$ - $C_i$  curves were carried out at a saturating PPFD level of 500 and 1300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for shaded, lower canopy and sunlit,  
249 upper canopy leaves, respectively. Verryckt et al. (2020a) showed that 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  is below light-saturation and a PPFD  
250 level of 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$  would have been optimal for shaded, lower canopy leaves. Increasing the PPFD level would, however,  
251 only result in a small increase of net photosynthesis.

252 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-  
253 biphosphate ( $J_{max}$ ) or triose phosphate use (TPU). These curves were fitted with the FvCB model using the fitaci function from  
254 the “Plantecophys” package (Duursma, 2015) in R 3.3.3 (R Core Team, 2019) to obtain the biochemical parameters  $V_{cmax}$ ,  $J_{max}$   
255 and, when possible, TPU.

#### 256 4.2.2 Light-saturated photosynthesis ( $A_{sat}$ ) of saplings

257 Light-saturated photosynthesis ( $A_{sat}$ ) and the stomatal conductance ( $g_s$ ) were measured, separately from the  $A_n$ - $C_i$  curves, for  
258 the saplings at the Paracou plots situated at the bottom valleys and hilltops. We used the methods described in protocol 2.1.3  
259 Leaf-scale photosynthesis and protocol 5.7 Stomatal conductance in the Supporting Information, respectively, S2 Carbon and  
260 nutrient cycling and S5 Stress physiology in Halbritter et al. (2020). The  $\text{CO}_2$  concentration was maintained at 400 ppm and a  
261 the PPFD was set at 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . In 2016,  $A_{sat}$  and  $g_s$  were measured on one leaf per individual and for three to five  
262 individuals per species. This resulted in a total of 159 measurements. In 2017, after 1-year of nutrient addition, these  
263 measurements were repeated on the same individuals when they survived, and on additional saplings resulting in 195  
264 measurements in total.

#### 265 4.3 Leaf traits

266 All leaves used for gas exchange were collected and, for the mature trees, leaf chlorophyll was estimated by averaging five  
267 chlorophyll content measurements from each leaf with a CCM-200 portable chlorophyll meter (Opti-Sciences, Tyngsborough,  
268 MA, USA), thereby avoiding major veins and areas of obvious visual damage or disease. A unitless chlorophyll content index  
269 (CCI) value was calculated from the ratio of optical absorbance at 655 nm to that at 940 nm. Then, the leaves were scanned to  
270 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,  
271 Lincoln, NE, USA), which, together with the leaf dry mass, was used to calculate the specific leaf area (SLA). After grinding  
272 the dried leaves, leaf nutrient concentrations were determined in accordance with protocol 2.1.6 Foliar nutrient stoichiometry  
273 and resorption in Supporting information S2 Carbon and nutrient cycling in Halbritter et al. (2020). Leaf C and N  
274 concentrations of 10 mg subsamples were determined by dry combustion using a Flash 2000 elemental analyzer (Thermo  
275 Fisher Scientific, Germany). Leaf P concentration of 0.1 g subsamples was determined by an acid digestion method (Walinga  
276 et al., 1989) on a Skalar SAN++ continuous flow analyzer, and thereafter analyzed on an iCAP 7400 radial optical emission



277 spectrometer (Thermo Fisher Scientific, Germany) to determine the concentration of leaf K, Ca, Mg, and Mn. Samples were  
278 ashed, digested with nitric acid (HNO<sub>3</sub>) and filtered prior to analysis.

279 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  
280 spectrometer (Agilent Technologies, Tokyo, Japan) after digestion with HNO<sub>3</sub>.

281 For saplings, total phenolic concentration of the leaves was measured using an improved Folin-Ciocalteu assay (Singleton  
282 and Rossi, 1965; Marigo, 1973) and total leaf tannin concentration of the leaves was determined with the butanol/HCl method  
283 (Porter et al., 1985) modified as in Makkar and Goodchild (1996). The extracts for both phenol and tannin concentrations were  
284 determined using a Helios Alpha spectrophotometer (Thermo Spectronic, Cambridge, UK) at 760 and 550 nm, respectively.  
285 Both methods are described in detail in Peñuelas et al. (2010).

#### 286 **4.4 Ancillary data**

287 The vertical structure of a tropical rainforest is complex and multi-layered, resulting in great variation in light availability  
288 within the canopy (Yoda, 1974). We assessed the light environment of each studied tree by visually estimating the canopy  
289 light exposure or Dawkins' crown illumination index (Dawkins, 1958). This index describes a tree's light environment based  
290 on a five-point scale ranging from (1) no direct light for suppressed trees to (5) crown fully illuminated for emergent trees  
291 (Figure 5).

292 Sampling height of the mature trees was measured with a Forestry Pro rangefinder (Nikon, Tokyo, Japan) by tree climbers  
293 situated at sampling height pointing towards the soil. For saplings, we measured the total height of the tree using a measuring  
294 tape, and additionally we measured the diameter at 10 cm and at 50 cm above surface level. On top of each sapling, we  
295 measured leaf area index (LAI) with the LAI-2000 (LI-COR, Lincoln, NE, USA) during periods of overcast sky.

296 Herbivory rates, i.e. foliar damage by herbivores, of the saplings was estimated as punctual herbivory (%) according to Pirk  
297 and Farji-Brener (2012). We visually assessed the missing area of the leaf and assigned each leaf to the following categories:  
298 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  
299 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)  
300 and dividing this result by the total number of leaves per sapling. To test the accuracy of this method, we photographed 106  
301 leaves we visually assessed and compared visual estimations of herbivory in the field using ImageJ. In 90% of the cases  
302 categories were well assigned.

#### 303 **5 Challenges of fieldwork in the tropics**

304 Fieldwork in the tropical rainforest is challenging because of its remoteness and extremely moist and warm climate. While  
305 Paracou is only a 45 min-drive from a major city, Kourou, Nouragues can only be reached by helicopter (30 min from Cayenne,  
306 the capital of French Guiana) or a combination of car (2 h from Cayenne) and motorized canoe (4-6 h from Regina to  
307 Nouragues). Carrying out fieldwork in such a remote location requires adequate logistical planning and funding, as both people



308 and material need to be transported to this remote site and stay there for prolonged periods. Proper planning and coordination  
309 with the whole team was required to get the fieldwork finished within a limited timeframe.

310 The combination of high temperature and humidity poses an additional hurdle as this generally makes physical exertion harder  
311 than in temperate climates and, most importantly, decreases the longevity of most if not all electronic devices. Indeed, we  
312 suffered from several Li-6400XT malfunctions, as well as defects of laptops, freezers and drying ovens. However, these defects  
313 did not reduce the reliability of our data, but it required extra precautions and increased expenses. We tested, for example, the  
314 Li-6400XT devices each morning and the devices were regularly cross-calibrated. Malfunctions of these devices led to  
315 troubleshooting and extra testing before new measurements were carried out, which can be very time consuming and did have  
316 an impact on the amount of data that could be gathered. Laptops and other electronic devices were best stored overnight in a  
317 waterproof bag/barrel, whereas regularly moving them in and out of air-conditioned rooms increased malfunctions.  
318 Additionally, access to power was limited and a portable generator was often required to carry out all photosynthesis  
319 measurements.

320 The tropical soil is hard, making it very labour intensive to take soil cores and posing several other problems. Soil corers  
321 deformed as they are not developed for tropical soil types and the installation of PRS probes without breaking them was very  
322 challenging. Another challenge is reaching upper canopy leaves up to > 50 m height above ground level, which required  
323 technical tree climbing skills and equipment from experienced tree climbers.

324 High species diversity and stand structural complexity of tropical forests are a major challenge to understand the ecosystem  
325 functioning of tropical forests and force researchers to study either some abundant species following them in time or to take  
326 into account the high diversity limiting the number of replicates per species.

## 327 **6 Data availability**

328 This Photosynthesis-Soil database is provided as an excel workbook and is freely available at DOI 10.5281/zenodo.4719242.  
329 Photosynthetic CO<sub>2</sub>-response curves are presented as raw  $A_n-C_i$  files which can be analyzed by any user of the database, but  
330  $V_{cmax}$  and  $J_{max}$  values, fitted using the “Plantecophys” package (Duursma, 2015) in R, can also be found in the database in  
331 addition to the leaf traits. The soil database of 2015, including bulk density, soil particle size distribution, soil moisture and  
332 nutrients, and the fertilizer composition are shown in separate sheets.

## 333 **7 Summary**

334 Publicly accessible and usable datasets from experimental sites are needed to greatly enhance the power of data synthesis as  
335 well as model development and evaluation (Vicca et al., 2018; Halbritter et al., 2020). We provide vertical profiles of  
336 photosynthetic capacity data and important leaf traits from two three-year large-scale nutrient addition experiments conducted  
337 in two tropical rainforests in French Guiana. Our dataset is extremely valuable to the modelling and tropical ecology



338 community as we present a valuable source of information to further improve model representations of the roles of leaf  
339 nutrients in photosynthesis in tropical forests. We present raw  $A_n-C_i$  curves, which allows the curves to be fit under the same  
340 assumptions as curves collected at other sites, avoiding bias in the method of analysis. In addition, we provide  $V_{cmax}$  and  $J_{max}$   
341 values making these values immediately available to the modelling community. We provide leaf-level photosynthesis data at  
342 several heights within the canopy from mature trees and saplings allowing to study differences in sunlit and shaded leaves.  
343 Ancillary data such as herbivory and leaf phenol concentration can be of great value as additional data to other studies on these  
344 topics. A large set of soil properties and nutrient availabilities in the soils underlying the studied trees were made available as  
345 these data are highly relevant to understand how and why nutrient availability interacts with C uptake in tropical forests.

#### 346 **Author contribution**

347 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.,  
348 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  
349 lab analysis. The manuscript was drafted by L.T.V., I.A.J. and S.V. and was further revised by all co-authors.

#### 350 **Competing interests**

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

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523 **Tables**

524 **Table 1 Overview of the number of  $A_n-C_i$  curves measured in this study. Measurements were carried out in the wet and dry season,**  
 525 **at different canopy levels (U = upper canopy, sunlit leaves; L = lower canopy, shaded leaves; M = middle canopy leaves), at different**  
 526 **field sites (Nouragues-Inselberg, Nouragues-Pararé, Paracou). The measurements carried out on saplings instead of on mature,**  
 527 **canopy trees are mentioned separately. Pre-treatment measured were carried out in 2015 and 2016, whereas post-treatment (after**  
 528 **1 year and 3 years of nutrient addition) were carried out in 2017 and 2019.**

	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	
<b>2015</b>	141	82	146	76				61	113	56	120	
<b>2016</b>								42		35		38
<b>2017</b>					37	45	32					46
<b>2019</b>	156		163					155		164		

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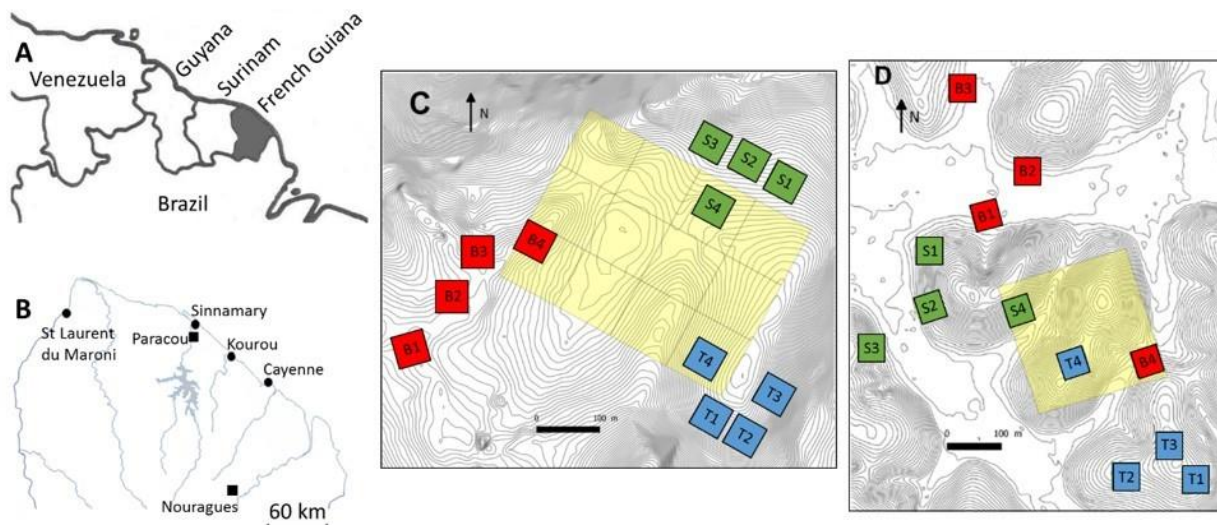
531 **Table 2 Overview of the amount of mature trees and species measured in each plot at Nouragues-Inselberg (NOU-I), Nouragues-**  
 532 **Pararé (NOU-P) and Paracou (PAR). Values between brackets indicate the amount of different species measured per plot, in case**  
 533 **this differed from the amount of trees measured per plot. Names of plots are marked by a letter describing the topography (B =**  
 534 **bottom, S = slope, T = top) and a number describing the nutrient addition treatment (1 = +N, 2 = +NP, 3 = +P, 4 = control), in**  
 535 **agreement with Figure 1C, D.**

		2015		2016	2017	2019	
		DRY	WET	WET	DRY	WET	
<b>NOU-I</b>	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	
	<b>NOU-P</b>	COPAS				12 (9)	
<b>PAR</b>	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	

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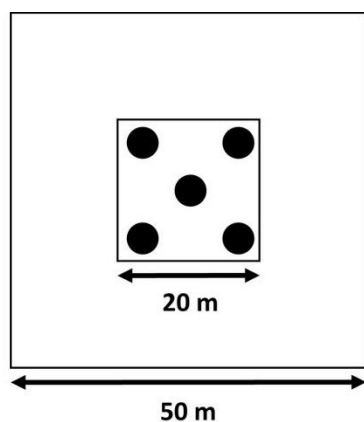


537 **Figures**



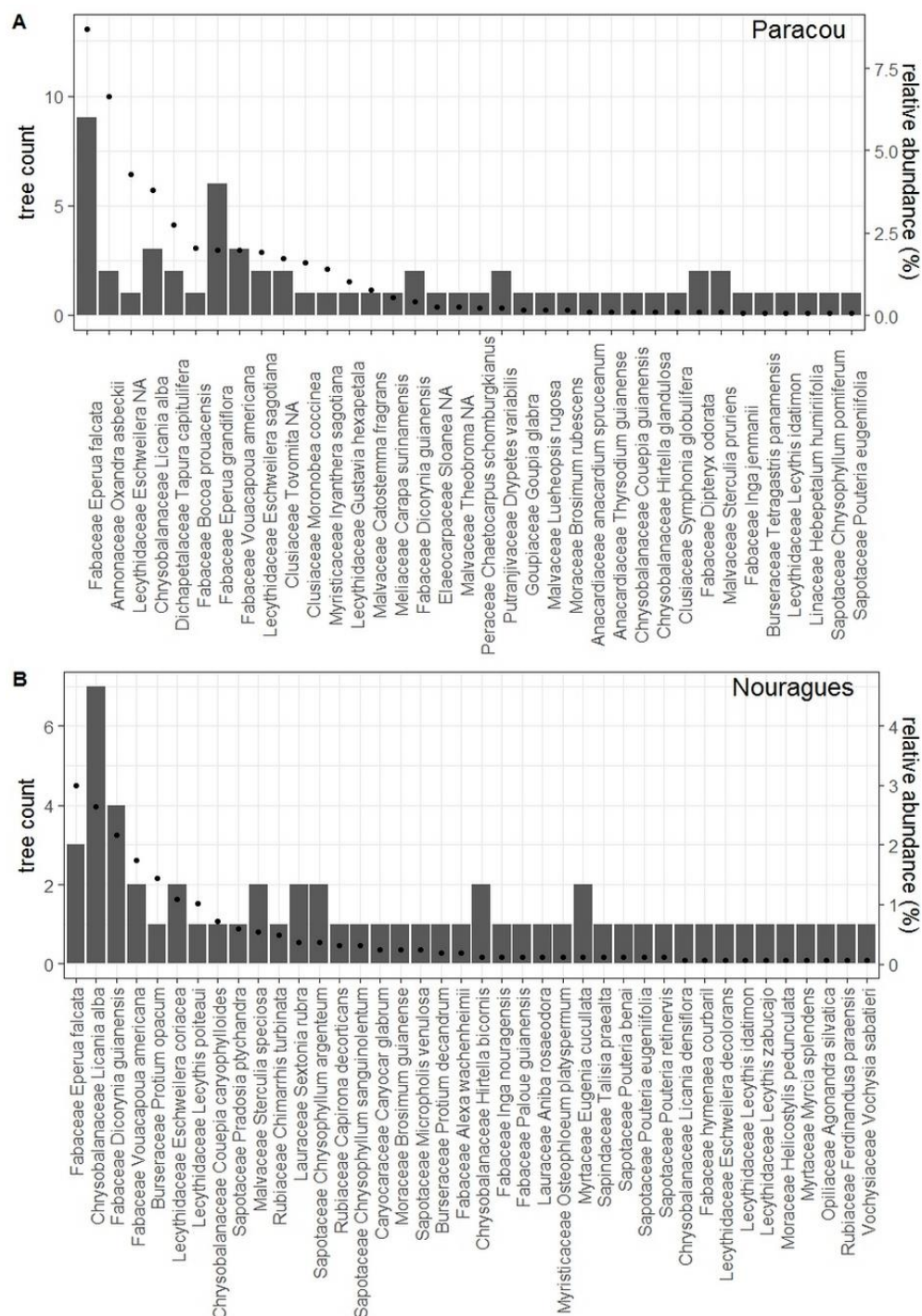
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539 **Figure 1** Situational map: (A) north-eastern part of South America, (B) northern French Guiana with its main cities (circles) and  
540 the experimental sites Paracou and Nouragues (closed squares), (C) the twelve study 50 x 50 m plots of this study at Nouragues-  
541 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).  
542 Plots are marked by a letter describing the topography (B = bottom, S = slope, T = top) and a number describing the nutrient  
543 addition treatment (1 = +N, 2 = +NP, 3 = +P, 4 = control).

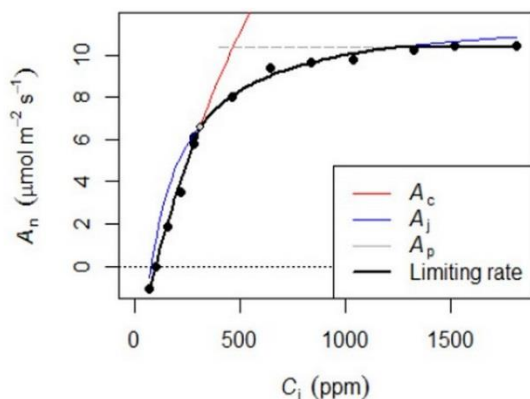


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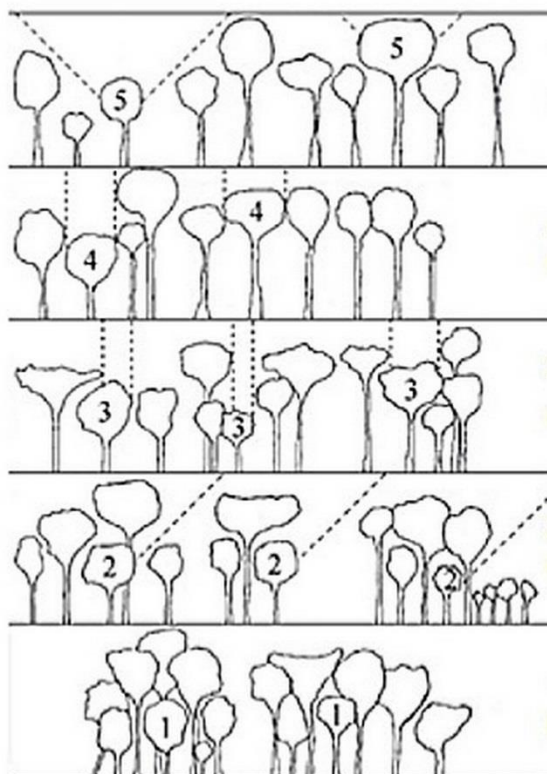
545 **Figure 2** Soil sampling design according to a 5-on-dice pattern, performed in the central 20 x 20 m area within each of the 50 x 50 m  
546 plots.



547  
 548 **Figure 3** Number of mature trees we sampled per species (bars) and the relative abundance for each species (dots) are shown for (A)  
 549 **Paracou** and (B) **Nouragues**. Relative abundance was calculated as the percent composition of each species relative to the total  
 550 number of that species with all 50 x 50 m plots at Paracou or Nouragues.



551  
552 **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:  
553 **rubisco ( $A_c$ ), RuBp ( $A_j$ ) or TPU ( $A_p$ ).**



554  
555 **Figure 5** Classification of the Dawkins' crown illumination index (adapted from Dawkins 1958): (1) no direct light, (2) low lateral  
556 light, (3) some vertical light (10-90% of the vertical projection of the crown exposed to vertical illumination), (4) crown completely  
557 exposed to vertical light, but lateral light blocked within some or all of the 90° inverted cone encompassing the crown (5) crown fully  
558 exposed to vertical and lateral illumination.