

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**

4 Lore T. Verryckt¹, Sara Vicca¹, Leandro Van Langenhove¹, Clément Stahl², Dolores Asensio^{3,4}, Ifigenia
5 Urbina^{3,4}, Romà Ogaya^{3,4}, Joan Llusà^{3,4}, Oriol Grau^{3,4,6}, Guille Peguero^{3,4}, Albert Gargallo-Garriga^{3,4,7},
6 Elodie A. Courtois⁸, Olga Margalef^{3,5}, Miguel Portillo-Estrada¹, Philippe Ciais⁹, Michael Obersteiner¹⁰,
7 Lucia Fuchslueger¹¹, Laynara F. Lugli¹², Pere-Roc Fernandez-Garberí^{3,4}, Helena Vallicrosa^{3,4}, Melanie
8 Verlinden¹, Christian Ranits¹¹, Pieter Vermeir¹³, Sabrina Coste¹⁴, Erik Verbruggen¹, Laëtitia Bréchet^{1,15},
9 Jordi Sardans^{3,4}, Jérôme Chave¹⁶, Josep Peñuelas^{3,4}, Ivan A. Janssens¹

10 ¹ Plants and Ecosystems (PLECO), Biology Department, University of Antwerp, Wilrijk, 2610, Belgium

11 ² UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRAE, Université des Antilles, Université de Guyane, Kourou, 97310,
12 France.

13 ³ CREAM, Campus Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, 08193, Catalonia, Spain.

14 ⁴ CSIC, Global Ecology Unit CREAM- CSIC-UAB, Bellaterra, Barcelona, 08193, Catalonia, Spain.

15 ⁵ RISKINAT Research Group, Department of Earth and Ocean Dynamics, University of Barcelona, Barcelona, 08028, Spain

16 ⁶ Cirad, UMR EcoFoG (AgroParisTech, CNRS, Inra, Univ Antilles, Univ Guyane), Campus Agronomique, Kourou, 97310,
17 French Guiana

18 ⁷ Global Change Research Institute, Czech Academy of Sciences, Bělidla 986/4a, Brno, 60300, Czech Republic.

19 ⁸ Laboratoire Ecologie, évolution, interactions des systèmes amazoniens (LEEISA), CNRS, IFREMER, Université de Guyane,
20 Cayenne, French Guiana

21 ⁹ Laboratoire des Sciences du Climat et de l'Environnement, CEA-CNRS-UVSQ, Gif-sur-Yvette, France

22 ¹⁰ International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

23 ¹¹ Centre for Microbiology and Environmental Systems Science (CMESS), University of Vienna, Vienna, 1090, Austria

24 ¹² Coordination of Environmental Dynamics, National Institute of Amazonian Research, Manaus, AM, 69060-062, Brazil

25 ¹³ Laboratory for Chemical Analysis (LCA), Department of Green Chemistry and Technology, Faculty of Bioscience
26 Engineering, Ghent University, Ghent, 9000, Belgium

27 ¹⁴ UMR EcoFoG, AgroParisTech, CIRAD, CNRS, INRAE , Université des Antilles, Université de Guyane, Kourou, 97310,
28 France

29 ¹⁵ INRA, UMR EcoFoG: Research Unit Ecology of Guianan Forests (CNRS, CIRAD, AgroParisTech, Université des Antilles,
30 Université de Guyane), Kourou, 97310, France

31 ¹⁶ Evolution et Diversité Biologique, CNRS, IRD, UPS, 118 route de Narbonne, Toulouse, 31062, France

32 *Correspondence to:* Lore T. Verryckt (lore.verryckt@uantwerpen.be)

33

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 (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) (Bonafant 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⁻¹ (2004 – 2015) (Aguilón et al., 2019). The average density of trees with a diameter

98 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).
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⁻¹ and tree density (DBH > 10 cm) averaged ca. 535 trees ha⁻¹ (Bongers et al., 2001). Tree species richness
103 ranges between 180 and 200 species ha⁻¹. 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 quartzites (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-richer soils of western Amazonia,
111 particularly low in P concentration (Table 1) (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 CO₂ 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. The monthly rainfall data measured at the instrumentation towers
115 of Paracou and Nouragues are shown in the dataset.

116 **2.2 Nutrient addition experiment**

117 **2.2.1 Set-up**

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

124 In October 2016, a field nutrient addition experiment at both sites was initiated and is ongoing to this day. In each block, one
125 plot served as control plot and the remaining three plots received one of three nutrient addition treatments (+N, +P or +NP).
126 Fertilizer was applied twice per year by hand-broadcasting commercial urea ((NH₂)₂CO) and/or triple superphosphate
127 (Ca(H₂PO₄)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
128 treatment). These application rates are identical as those in the ongoing nutrient addition experiment in Barro Colorado Nature
129 Monument in Panama, which was initiated in 1998 (Wright et al., 2011), and the Amazon Fertilization Experiment (AFEX)

130 near Manaus in Brazil, initiated in 2017 (Lugli et al., 2021), to enable future comparison of our results. In Paracou, these rates
131 of nutrient addition represent, respectively, 130% and 250% of yearly N and P input through litterfall and atmospheric
132 deposition combined (Van Langenhove et al., 2020b).
133 Leaf and soil sampling took place before (in 2015) and after a three-year period (in 2019) of the nutrient addition experiment.
134 To avoid border effects of the nutrient addition, these measurements were conducted in the central 20 x 20 m area within the
135 larger 50 x 50 m plots.

136 **2.2.2 Fertilizer composition**

137 Within the nutrient addition experiment, N was added as commercial urea ($(\text{NH}_2)_2\text{CO}$) and P as triple superphosphate
138 ($\text{Ca}(\text{H}_2\text{PO}_4)_2$). The chemical composition of the applied fertilizers was analyzed to know the exact composition. Samples of
139 both fertilizers were dried at 70°C for 48 h, after which they were ground. Total N of the fertilizers was determined by dry
140 combustion using a Skalar Primacs (Skalar Holding, The Netherlands). P_2O_5 and MgO in mineral acid were determined by
141 an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany). The ground samples were analyzed
142 with an iCAP 7400 radial optical emission spectrometer (Thermo Fisher Scientific, Germany) to determine the potassium (K),
143 calcium (Ca) and magnesium (Mg) concentrations, as well as the heavy metal concentrations (arsenic (As), cadmium (Cd),
144 chromium (Cr), copper (Cu), iron (Fe), nickel (Ni), lead (Pb), zinc (Zn), molybdenum (Mo)).

145 **3 Data and Methods: soil sampling**

146 **3.1 Sampling design**

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

157 **3.2 Soil physical properties**

158 **3.2.1 Bulk density**

159 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
160 sieved through a 2-mm sieve. We collected the soil fraction, the roots and the stones, which were dried and weighed separately
161 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
162 soil core divided by its volume (i.e. the volume of the auger, 754 cm³), whereas exclusive bulk density is calculated by dividing
163 the total weight of the soil fraction (excluding roots and stones) by the volume of the entire core (i.e. 754 cm³).

164 **3.2.1 Soil particle size distribution**

165 The particle size distribution at plot level was analysed only in the wet season of 2015, assuming it would not change with
166 seasonality. Therefore, we mixed by hand the five samples per plot that were sieved (< 2 mm) after extraction using a gouge
167 auger, and analyzed these mixed samples as one composite sample per depth and per plot. We determined the soil particle size
168 distribution using sedimentation with the hydrometer method (Gee and Bauder, 1986) after SOM oxidation with H₂O₂, as
169 described in protocol 1.3.5 Soil texture in the Supporting information S1 Site characteristics and data management in Halbritter
170 et al. (2020). Soil particles were dispersed with sodium hexametaphosphate and the quantity of sand, silt and clay were
171 determined using a hydrometer.

172 **3.2.3 Soil moisture**

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

176 **3.3 Soil nutrients**

177 **3.3.1 Chemical analyses: concentrations and availability**

178 Freshly sieved soil was used for the measurement of pH and the extraction of inorganic N (N_i) and inorganic P (P_i). We
179 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
180 ratio and shaking it for 1 h. The same solution was passed through a 42-µm filter and the filtrate's concentration of NH₄⁺ and
181 NO₃⁻ was determined colourimetrically (SAN++ continuous flow analyzer, Skalar Inc., The Netherlands). The P_i was extracted
182 with the Olsen-P bicarbonate extraction (Olsen et al., 1954) and measured on an iCAP 6300 Duo ICP optical emission
183 spectrometer (Thermo Fisher Scientific, Germany).

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

186 by analysis on an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany). Water soluble
187 molybdate (MoO_4^{2-}) and phosphate (PO_4^{3-}) were determined through resin extraction on previously dried (60°C) soil
188 (Wurzburger et al., 2012). The soil samples were mixed with water in a 1:6 ratio and five 2-cm² strips of anion-exchange
189 membrane (VWR Chemicals, USA) were added (Van Langenhove et al., 2019; Wurzburger et al., 2012). After stirring this
190 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
191 analyzed with an iCAP 6300 Duo ICP optical emission spectrometer (Thermo Fisher Scientific, Germany).

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

198 **3.3.2 PRS probes**

199 We used Plant Root Simulator (PRS ®) probes (Western Ag Innovations Inc., Saskatoon, CA) to provide proxies for plant
200 available ions in soil solution (Van Langenhove et al., 2020a; Halbritter et al., 2020). These PRS probes are ion exchange resin
201 membranes (IEM; approximately 5.5 cm × 1.6 cm, or 17.5 cm² including both sides of the IEM) held in plastic supports that
202 were vertically inserted into soil with minimal disturbance (Hangs et al., 2004). In each plot, we installed five root exclusion
203 cylinders (REC) following a five-on-a-dice design to study soil nutrient dynamics in absence of the root system (Van
204 Langenhove et al., 2020a). RECs were PVC collars inserted 20 cm into the soil to sever all near-surface roots and mycorrhizal
205 fungal hyphae, and were installed prior to the first soil nutrient measurements in May 2015.

206 In both the wet (May) and dry (October) season of 2015, we installed four anion and four cation probes, which formed one
207 sample, into each REC. After a period of two weeks, the PRSTM probes were removed from the soil, washed with distilled
208 water and shipped to the manufacturer for analysis of the following nutrients: P, K, Ca, Mg, S, Mn, Cd, Cu, Fe, Pb, Zn, nitrate
209 (NO_3), ammonium (NH_4), boron (B) and aluminium (Al). In situ burial of the PRSTM probes provide a dynamic measure of
210 nutrient flux, or nutrient supply rate to an ion sink (Gibson et al., 1985; Casals et al., 1995). The results are thus expressed as
211 the amount of nutrient adsorbed per surface area of IEM during the duration of burial (Qian and Schoenau, 2002). In our study
212 it was expressed as μg nutrient 10 cm⁻².for two weeks.

213 **4 Data and Methods: leaf sampling**

214 **4.1 Tree selection**

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

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

221 **4.2 Photosynthesis**

222 **4.2.1 Leaf gas exchange**

223 We measured leaf gas exchange measurements using a set of infrared gas analyzers (IRGAs) incorporated into a portable
224 photosynthesis system (LI-6400XT, LI-COR, Lincoln, NE, USA). A leaf was clamped within a chamber with controlled
225 microenvironmental conditions during the measurements and the device measures the concentration changes of water vapour
226 (H₂O) and carbon dioxide (CO₂) between incoming and outgoing air. The relative humidity inside the chamber (67.9 % ± 0.06)
227 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
228 block temperature was controlled to minimize variation in leaf temperature and was set at 30.1 ± 0.9°C.

229 Pre-treatment measurements of the mature trees were carried out in both wet (May-June) and dry season (October-November)
230 of 2015, except for the wet season measurements of the plots at Paracou situated at the slope which were measured in June
231 2016 due to practical constraints. After three years of nutrient addition, we repeated the leaf gas exchange measurements of
232 the mature trees in the wet season (May-June) of 2019. We measured leaf gas exchange of leaves collected at two different
233 canopy heights, estimated relative to the top of the canopy: sunlit, upper canopy foliage and shaded, lower canopy foliage.
234 Branch excision prior to measuring leaf gas exchange was necessary to reach the canopy leaves. The excised branches (ca.
235 2 m-long) were cut by a tree climber and immediately recut under water to restore hydraulic conductivity (Domingues et al.,
236 2010; Dusenge et al., 2015; Rowland et al., 2015; Verryckt et al., 2020b). Photosynthesis measurements of the saplings were
237 carried out on leaves still attached to the trees and were performed in August 2016 (pre-treatment) and August 2017 (1-year
238 of nutrient addition). All photosynthesis measurements were conducted between 09:00 and 16:00 (local time).

239 **4.2.1 Photosynthetic CO₂-response curves**

240 Photosynthetic CO₂-response curves (Figure 4) were established by measuring net photosynthetic rates (A_n) at different CO₂
241 concentrations by controlling the reference CO₂ concentrations, while maintaining a constant temperature and photosynthetic
242 photon flux density (PPFD). The A_n - C_i (C_i , the CO₂ concentration of the leaf intercellular spaces) measurements began at the
243 ambient CO₂ concentration of 400 ppm. Once a steady state of photosynthesis was reached, the CO₂ concentrations was
244 reduced stepwise to 50 ppm, then returned to 400 ppm, and thereafter increased to 2000 ppm, to obtain a total of 10-14
245 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
246 measured (Table 3). The methods used here are described in protocol 2.1.3 Leaf-scale photosynthesis in the Supporting

247 Information S2 Carbon and nutrient cycling in Halbritter et al. (2020). Additionally, we measured leaf dark respiration (R_d) by
248 taking five consecutive measurements on one leaf per branch level, after keeping the branch in complete darkness for 30 min.
249 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,
250 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
251 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,
252 only result in a small increase of net photosynthesis.

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

257 **4.2.2 Light-saturated photosynthesis (A_{sat}) of saplings**

258 Light-saturated photosynthesis (A_{sat}) and the stomatal conductance (g_s) were measured, separately from the A_n - C_i curves, for
259 the saplings at the Paracou plots situated at the bottom valleys and hilltops. We used the methods described in protocol 2.1.3
260 Leaf-scale photosynthesis and protocol 5.7 Stomatal conductance in the Supporting Information, respectively, S2 Carbon and
261 nutrient cycling and S5 Stress physiology in Halbritter et al. (2020). The CO_2 concentration was maintained at 400 ppm and a
262 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
263 individuals per species. This resulted in a total of 159 measurements. In 2017, after 1-year of nutrient addition, these
264 measurements were repeated on the same individuals when they survived, and on additional saplings resulting in 195
265 measurements in total.

266 **4.3 Leaf traits**

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

278 spectrometer (Thermo Fisher Scientific, Germany) to determine the concentration of leaf K, Ca, Mg, and Mn. Samples were
279 ashed, digested with nitric acid (HNO₃) and filtered prior to analysis.
280 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
281 spectrometer (Agilent Technologies, Tokyo, Japan) after digestion with HNO₃.
282 For saplings, total phenolic concentration of the leaves was measured using an improved Folin-Ciocalteu assay (Singleton
283 and Rossi, 1965; Marigo, 1973) and total leaf tannin concentration of the leaves was determined with the butanol/HCl method
284 (Porter et al., 1985) modified as in Makkar and Goodchild (1996). The extracts for both phenol and tannin concentrations were
285 determined using a Helios Alpha spectrophotometer (Thermo Spectronic, Cambridge, UK) at 760 and 550 nm, respectively.
286 Both methods are described in detail in Peñuelas et al. (2010).

287 **4.4 Ancillary data**

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

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

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

304 **5 V_{max} of sunlit, upper canopy leaves**

305 TBMs use plant functional types (PFT) to represent broad groupings of plant species that share similar characteristics (e.g.
306 growth form) and roles (e.g. photosynthetic pathway) in ecosystem function (Rogers et al., 2017). Although all TBMs share
307 this approach, they differ from each other in how narrow or broad the PFTs are defined. Depending on the TBM, tropical
308 rainforests belong to "broadleaf evergreen tropical tree", "tropical tree", "rainforest", "evergreen broadleaf tree" or "broadleaf

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

316 **6 Challenges of fieldwork in the tropics**

317 Fieldwork in the tropical rainforest is challenging because of its remoteness and extremely moist and warm climate. While
318 Paracou is only a 45 min-drive from a major city, Kourou, Nouragues can only be reached by helicopter (30 min from Cayenne,
319 the capital of French Guiana) or a combination of car (2 h from Cayenne) and motorized canoe (4-6 h from Regina to
320 Nouragues). Carrying out fieldwork in such a remote location requires adequate logistical planning and funding, as both people
321 and material need to be transported to this remote site and stay there for prolonged periods. Proper planning and coordination
322 with the whole team was required to get the fieldwork finished within a limited timeframe.

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

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

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

340 **7 Data availability**

341 This Photosynthesis-Soil database is provided as an excel workbook and is freely available at DOI 10.5281/zenodo.5638236.
342 Photosynthetic CO₂-response curves are presented as raw A_n-C_i files which can be analyzed by any user of the database, but
343 V_{cmax} and J_{max} values, fitted using the “Plantecophys” package (Duursma, 2015) in R, can also be found in the database in
344 addition to the leaf traits. The soil database of 2015, including bulk density, soil particle size distribution, soil moisture and
345 nutrients, and the fertilizer composition are shown in separate sheets.

346 **8 Summary**

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

359 **Author contribution**

360 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.,
361 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
362 lab analysis. The manuscript was drafted by L.T.V., I.A.J. and S.V. and was further revised by all co-authors.

363 **Competing interests**

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

365 Acknowledgements

366 L. T. Verryckt is funded by a PhD fellowship from the Research Foundation Flanders (FWO). This project was funded by the
367 European Research Council Synergy Grant; ERC-2013-SyG-610028 IMBALANCE-P. We thank the staff of the Nouragues
368 Ecological Research Station, managed by USR mixte LEEISA (CNRS; Cayenne), and the Paracou station, managed by UMR
369 Ecofog (CIRAD, INRA; Kourou). Both research stations received support from “Investissement d’Avenir” grants managed by
370 Agence Nationale de la Recherche (CEBA: ANR-10-LABX-25-01, AnaEE-France: ANR-11-INBS-0001).
371 We are grateful to Valentine Alt, Samuel Counil, Jocelyn Cazal, Gonzalo Carrillo, Jean-Loup Touchard, Anthony Percevaux,
372 Benjamin Leudet and Stefan van Beveren for climbing the trees to collect the selected branches.

373 References

- 374 Aguilos, M., Stahl, C., Burban, B., Hérault, B., Courtois, E., Coste, S., Wagner, F., Ziegler, C., Takagi, K., and Bonal, D.: Interannual and
375 Seasonal Variations in Ecosystem Transpiration and Water Use Efficiency in a Tropical Rainforest, *Forests*, 10, 14, 2019.
- 376 Bahar, N. H., Ishida, F. Y., Weerasinghe, L. K., Guerrieri, R., O’Sullivan, O. S., Bloomfield, K. J., Asner, G. P., Martin, R. E., Lloyd, J.,
377 Malhi, Y., Phillips, O. L., Meir, P., Salinas, N., Cosio, E. G., Domingues, T. F., Quesada, C. A., Sinca, F., Escudero Vega, A., Zuloaga
378 Ccorimanya, P. P., Del Aguila-Pasquel, J., Quispe Huaypar, K., Cuba Torres, I., Butron Loayza, R., Pelaez Tapia, Y., Huaman Ovalle, J.,
379 Long, B. M., Evans, J. R., and Atkin, O. K.: Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation Andean tropical
380 moist forests of Peru, *New Phytologist*, 214, 1002-1018, 10.1111/nph.14079, 2016.
- 381 Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Altaf Arain, M., Baldocchi, D., Bonan, G. B.,
382 Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luysaert, S., Margolis, H., Oleson, K. W., Rouspard, O., Veenendaal, E.,
383 Viovy, N., Williams, C., Woodward, F. I., and Papale, D.: Terrestrial Gross Carbon Dioxide Uptake - global distribution and variation with
384 climate, *Science*, 329, 834-838, 10.1126/science.1184984, 2010.
- 385 Berry, Z. C., and Goldsmith, G. R.: Diffuse light and wetting differentially affect tropical tree leaf photosynthesis, *New Phytologist*, 225,
386 143-153, <https://doi.org/10.1111/nph.16121>, 2020.
- 387 Bonal, D., Bosc, A., Ponton, S., Goret, J.-Y., Burban, B., Gross, P., Bonnefond, J.-M., Elbers, J. A. N., Longdoz, B., Epron, D., Guehl, J.-
388 M., and Granier, A.: Impact of severe dry season on net ecosystem exchange in the Neotropical rainforest of French Guiana, *Global Change*
389 *Biology*, 14, 1917-1933, 10.1111/j.1365-2486.2008.01610.x, 2008.
- 390 Bonan, G.: *Ecological Climatology: Concepts and Applications*, 3 ed., Cambridge University Press, Cambridge, 2015.
- 391 Bongers, F., Charles-Dominique, P., Forget, P.-M., and Théry, M.: *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical*
392 *Rainforest*, Kluwer Academic Publishers, Dordrecht, The Netherlands, 2001.
- 393 Bray, R. H., and Kurtz, L. T.: Determination of total, organic and available forms of phosphorus in soils, *Soil Science*, 59, 39-46, 1945.
- 394 Casals, P., Romanyà, J., Cortina, J., Fons, J., Bode, M., and Vallejo, V. R.: Nitrogen supply rate in Scots pine (*Pinus sylvestris* L.) forests of
395 contrasting slope aspect, *Plant and Soil*, 168, 67-73, 1995.
- 396 Courtois, E. A., Stahl, C., Van den Berge, J., Bréchet, L., Van Langenhove, L., Richter, A., Urbina, I., Soong, J. L., Peñuelas, J., and Janssens,
397 I. A.: Spatial Variation of Soil CO₂, CH₄ and N₂O Fluxes Across Topographical Positions in Tropical Forests of the Guiana Shield,
398 *Ecosystems*, 21, 1445-1458, 10.1007/s10021-018-0232-6, 2018.
- 399 Dawkins, H. C.: *The management of tropical high forest with special reference to Uganda*, Tropical Forestry Paper 34, Imperial Forestry
400 Institute, Oxford, UK, 1958.
- 401 Domingues, T. F., Meir, P., Feldpausch, T. R., Saiz, G., Veenendaal, E. M., Schrod, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H.,
402 Diallo, A., Grace, J., and Lloyd, J.: Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands, *Plant*,
403 *Cell and Environment*, 33, 959-980, 10.1111/j.1365-3040.2010.02119.x, 2010.
- 404 Dusenge, M. E., Walling, G., Gärdesten, J., Nyronzima, F., Adolfsson, L., Nsabimana, D., and Uddling, J.: Photosynthetic capacity of
405 tropical montane tree species in relation to leaf nutrients, successional strategy and growth temperature, *Oecologia*, 117, 1183-1194,
406 10.1007/s00442-015-3260-3, 2015.
- 407 Duursma, R. A.: Plantecophys - An R Package for Analysing and Modelling Leaf Gas Exchange Data, *PLOS ONE*, 10, e0143346,
408 10.1371/journal.pone.0143346, 2015.
- 409 Epron, D., Bosc, A., Bonal, D., and Freycon, V.: Spatial variation of soil respiration across a topographic gradient in a tropical rain forest in
410 French Guiana, *Journal of Tropical Ecology*, 22, 565, 10.1017/s0266467406003415, 2006.

411 Farquhar, G. D., Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species, *Planta*,
412 149, 78-90, 10.1007/BF00386231, 1980.

413 Ferry, B., Morneau, F. o., Bontemps, J.-D., Blanc, L., and Freycon, V.: Higher treefall rates on slopes and waterlogged soils result in lower
414 stand biomass and productivity in a tropical rain forest, *Journal of Ecology*, 98, 106-116, 10.1111/j.1365-2745.2009.01604.x, 2010.

415 Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., Garcia, S., Goll, D. S., Grandis, A., Jiang,
416 M., Haverd, V., Hofhansl, F., Holm, J. A., Kruijt, B., Leung, F., Medlyn, B. E., Mercado, L. M., Norby, R. J., Pak, B., von Randow, C.,
417 Quesada, C. A., Schaap, K. J., Valverde-Barrantes, O. J., Wang, Y.-P., Yang, X., Zaehle, S., Zhu, Q., and Lapola, D. M.: Amazon forest
418 response to CO₂ fertilization dependent on plant phosphorus acquisition, *Nature Geoscience*, 12, 736-741, 10.1038/s41561-019-0404-9,
419 2019.

420 Gee, G. W., and Bauder, J. W.: Particle-size analysis, in: *Methods of Soil Analysis Part 1: Physical and Mineralogical Methods*, edited by:
421 Kute, A., American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA, 1986.

422 Gibson, D. J., Colquhoun, I. A., and Greig-Smith, P.: New method for measuring nutrient supply rates in soils using ion-exchange resins,
423 *Special publications series of the British Ecological Society*, 6, 1985.

424 Gourlet-Fleury, S., Guehl, J.-M., and Laroussinie, O.: *Ecology and management of a neotropical rainforest: lessons drawn from Paracou, a
425 long-term experimental research site in French Guiana*, Elsevier, Paris, 336 pp., 2004.

426 Grau, O., Penuelas, J., Ferry, B., Freycon, V., Blanc, L., Desprez, M., Baraloto, C., Chave, J., Descroix, L., Dourdain, A., Guitet, S., Janssens,
427 I. A., Sardans, J., and Herault, B.: Nutrient-cycling mechanisms other than the direct absorption from soil may control forest structure and
428 dynamics in poor Amazonian soils, *Sci Rep*, 7, 45017, 10.1038/srep45017, 2017.

429 Guitet, S., Freycon, V., Brunaux, O., Pélissier, R., Sabatier, D., and Coutron, P.: Geomorphic control of rain-forest floristic composition in
430 French Guiana: more than a soil filtering effect?, *Journal of Tropical Ecology*, 32, 22-40, 10.1017/S0266467415000620, 2016.

431 Halbritter, A. H., De Boeck, H. J., Eycott, A. E., Reinsch, S., Robinson, D. A., Vicca, S., Berauer, B., Christiansen, C. T., Estiarte, M.,
432 Grünzweig, J. M., Gya, R., Hansen, K., Jentsch, A., Lee, H., Linder, S., Marshall, J., Peñuelas, J., Kappel Schmidt, I., Stuart-Haëntjens, E.,
433 Wilfahrt, P., Group, t. C. W., and Vandvik, V.: The handbook for standardized field and laboratory measurements in terrestrial climate
434 change experiments and observational studies (ClimEx), *Methods in Ecology and Evolution*, 11, 22-37, [https://doi.org/10.1111/2041-
435 210X.13331](https://doi.org/10.1111/2041-210X.13331), 2020.

436 Hammond, D.: *Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World*, CABI Publishing, Cambridge, 2005.

437 Hangs, R. D., Greer, K. J., and Sulewski, C. A.: The effect of interspecific competition on conifer seedling growth and nitrogen availability
438 measured using ion-exchange membranes, *Canadian Journal of Forest Research*, 34, 754-761, 2004.

439 Lugli, L. F., Rosa, J. S., Andersen, K. M., Di Ponzio, R., Almeida, R. V., Pires, M., Cordeiro, A. L., Cunha, H. F. V., Martins, N. P., Assis,
440 R. L., Moraes, A. C. M., Souza, S. T., Aragão, L. E. O. C., Camargo, J. L., Fuchslueger, L., Schaap, K. J., Valverde-Barrantes, O. J., Meir,
441 P., Quesada, C. A., Mercado, L. M., and Hartley, I. P.: Rapid responses of root traits and productivity to phosphorus and cation additions in a
442 tropical lowland forest in Amazonia, *New Phytologist*, 230, 116-128, <https://doi.org/10.1111/nph.17154>, 2021.

443 Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü.,
444 Ordonez, A., Reich, P. B., and Santiago, L. S.: Global effects of soil and climate on leaf photosynthetic traits and rates, *Global Ecology and
445 Biogeography*, 24, 706-717, <https://doi.org/10.1111/geb.12296>, 2015.

446 Makkar, H. P. S., and Goodchild, A. V.: *Quantification of tannins: a laboratory manual*, International Center for Agricultural Research in
447 the Dry Area (ICARDA), Aleppo, 1996.

448 Malhi, Y.: The carbon balance of tropical forest regions, 1990–2005, *Current Opinion in Environmental Sustainability*, 2, 237-244,
449 10.1016/j.cosust.2010.08.002, 2010.

450 Medlyn, B. E., Zaehle, S., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hanson, P. J., Hickler, T., Jain, A. K., Luo, Y., Parton, W.,
451 Prentice, I. C., Thornton, P. E., Wang, S., Wang, Y.-P., Weng, E., Iversen, C. M., McCarthy, H. R., Warren, J. M., Oren, R., and Norby, R.
452 J.: Using ecosystem experiments to improve vegetation models, *Nature Climate Change*, 5, 528-534, 10.1038/nclimate2621, 2015.

453 Mo, Q., Li, Z. a., Sayer, E. J., Lambers, H., Li, Y., Zou, B., Tang, J., Heskell, M., Ding, Y., and Wang, F.: Foliar phosphorus fractions reveal
454 how tropical plants maintain photosynthetic rates despite low soil phosphorus availability, *Functional Ecology*, 33, 503-513, 10.1111/1365-
455 2435.13252, 2019.

456 Norby, R. J., Gu, L., Haworth, I. C., Jensen, A. M., Turner, B. L., Walker, A. P., Warren, J. M., Weston, D. J., Xu, C., and Winter, K.:
457 Informing models through empirical relationships between foliar phosphorus, nitrogen and photosynthesis across diverse woody species in
458 tropical forests of Panama, *New Phytologist*, 215, 1425-1437, <https://doi.org/10.1111/nph.14319>, 2017.

459 Olsen, S. R., Cole, C. V., and Watanabe, F. S.: Estimation of available phosphorus in soils by extraction with sodium bicarbonate, *Circular
460 / United States Department of Agriculture;no. 939*, USDA, Washington, 1954.

461 Peñuelas, J., Sardans, J., Llusia, J., Owen, S. M., Silva, J., and Niinemets, Ü.: Higher Allocation to Low Cost Chemical Defenses in Invasive
462 Species of Hawaii, *Journal of Chemical Ecology*, 36, 1255-1270, 10.1007/s10886-010-9862-7, 2010.

463 Pirk, G. I., and Farji-Brener, A. G.: Foliar herbivory and its effects on plant growth in native and exotic species in the Patagonian steppe,
464 *Ecological Research*, 27, 903-912, 10.1007/s11284-012-0968-y, 2012.

465 Porter, L. J., Hrstich, L. N., and Chan, B. G.: The conversion of procyanidins and prodelphinidins to cyanidin and delphinidin,
466 *Phytochemistry*, 25, 223-230, [https://doi.org/10.1016/S0031-9422\(00\)94533-3](https://doi.org/10.1016/S0031-9422(00)94533-3), 1985.

467 Qian, P., and Schoenau, J. J.: Practical applications of ion exchange resins in agricultural and environmental soil research, *Canadian Journal*
468 *of Soil Science*, 82, 9-21, 2002.

469 R Core Team: R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria, 2019.

470 Rogers, A.: The use and misuse of Vcmax in Earth System Models, *Photosynthesis Research*, 119, 15-29, 10.1007/s11120-013-9818-1,
471 2014.

472 Rowland, L., Lobo-do-Vale, R. L., Christoffersen, B. O., Melem, E. A., Kruijt, B., Vasconcelos, S. S., Domingues, T., Binks, O. J., Oliveira,
473 A. A., Metcalfe, D., da Costa, A. C., Mencuccini, M., and Meir, P.: After more than a decade of soil moisture deficit, tropical rainforest trees
474 maintain photosynthetic capacity, despite increased leaf respiration, *Global Change Biology*, 21, 4662-4672, 10.1111/gcb.13035, 2015.

475 Ruiz-Benito, P., Vacchiano, G., Lines, E. R., Reyer, C. P. O., Ratcliffe, S., Morin, X., Hartig, F., Mäkelä, A., Yousefpour, R., Chaves, J. E.,
476 Palacios-Orueta, A., Benito-Garzón, M., Morales-Molino, C., Camarero, J. J., Jump, A. S., Kattge, J., Lehtonen, A., Ibrom, A., Owen, H. J.
477 F., and Zavala, M. A.: Available and missing data to model impact of climate change on European forests, *Ecological Modelling*, 416,
478 108870, <https://doi.org/10.1016/j.ecolmodel.2019.108870>, 2020.

479 Singleton, V. L., and Rossi, J. A.: Colorimetry of Total Phenolics with Phosphomolybdic-Phosphotungstic Acid Reagents, *American Journal*
480 *of Enology and Viticulture*, 16, 144-158, 1965.

481 van der Meer, P. J., and Bongers, F.: Patterns of Tree-Fall and Branch-Fall in a Tropical Rain Forest in French Guiana, *Journal of Ecology*,
482 84, 19-29, 10.2307/2261696, 1996.

483 Van Der Meer, P. J., Sterck, F. J., and Bongers, F.: Tree seedling performance in canopy gaps in a tropical rain forest at Nouragues, French
484 Guiana, *Journal of Tropical Ecology*, 14, 119-137, 10.1017/S026646749800011X, 1998.

485 Van Langenhove, L., Depaepe, T., Vicca, S., van den Berge, J., Stahl, C., Courtois, E., Weedon, J., Urbina, I., Grau, O., Asensio, D.,
486 Peñuelas, J., Boeckx, P., Richter, A., Van Der Straeten, D., and Janssens, I. A.: Regulation of nitrogen fixation from free-living organisms
487 in soil and leaf litter of two tropical forests of the Guiana shield, *Plant and Soil*, 10.1007/s11104-019-04012-1, 2019.

488 Van Langenhove, L., Janssens, I. A., Verryckt, L., Brechet, L., Hartley, I. P., Stahl, C., Courtois, E., Urbina, I., Grau, O., Sardans, J., Peguero,
489 G., Gargallo-Garriga, A., Peñuelas, J., and Vicca, S.: Rapid root assimilation of added phosphorus in a lowland tropical rainforest of French
490 Guiana, *Soil Biology and Biochemistry*, 140, 107646, <https://doi.org/10.1016/j.soilbio.2019.107646>, 2020a.

491 Van Langenhove, L., Verryckt, L. T., Bréchet, L., Courtois, E. A., Stahl, C., Hofhansl, F., Bauters, M., Sardans, J., Boeckx, P., Fransen, E.,
492 Peñuelas, J., and Janssens, I. A.: Atmospheric deposition of elements and its relevance for nutrient budgets of tropical forests,
493 *Biogeochemistry*, 149, 175-193, 10.1007/s10533-020-00673-8, 2020b.

494 Van Langenhove, L., Verryckt, L. T., Stahl, C., Courtois, E. A., Urbina, I., Grau, O., Asensio, D., Peguero, G., Margalef, O., Freycon, V.,
495 Peñuelas, J., and Janssens, I. A.: Soil nutrient variation along a shallow catena in Paracou, French Guiana, *Soil Research*, 59, 130-145,
496 <https://doi.org/10.1071/SR20023>, 2020c.

497 Verryckt, L. T., Ellsworth, D. S., Vicca, S., Van Langenhove, L., Peñuelas, J., Ciais, P., Posada, J. M., Stahl, C., Coste, S., Courtois, E. A.,
498 Obersteiner, M., Chave, J., and Janssens, I. A.: Can light-saturated photosynthesis in lowland tropical forests be estimated by one light level?,
499 *Biotropica*, 52, 1183-1193, 10.1111/btp.12817, 2020a.

500 Verryckt, L. T., Van Langenhove, L., Ciais, P., Courtois, E. A., Vicca, S., Peñuelas, J., Stahl, C., Coste, S., Ellsworth, D. S., Posada, J. M.,
501 Obersteiner, M., Chave, J., and Janssens, I. A.: Coping with branch excision when measuring leaf net photosynthetic rates in a lowland
502 tropical forest, *Biotropica*, 52, 608-615, 10.1111/btp.12774, 2020b.

503 Verryckt, L. T.: Vertical profiles of leaf photosynthesis and leaf traits, and soil nutrients in two tropical rainforests in French Guiana before
504 and after a three-year nitrogen and phosphorus addition experiment [Data set], <http://doi.org/10.5281/zenodo.5638236>, 2021.

505 Vicca, S., Stocker, B. D., Reed, S., Wieder, W. R., Bahn, M., Fay, P. A., Janssens, I. A., Lambers, H., Peñuelas, J., Piao, S., Rebel, K. T.,
506 Sardans, J., Sigurdsson, B. D., Van Sundert, K., Wang, Y.-P., Zaehle, S., and Ciais, P.: Using research networks to create the comprehensive
507 datasets needed to assess nutrient availability as a key determinant of terrestrial carbon cycling, *Environmental Research Letters*, 13, 125006,
508 10.1088/1748-9326/aaeae7, 2018.

509 Vitousek, P. M., and Howarth, R. W.: Nitrogen limitation on land and in the sea: How can it occur?, *Biogeochemistry*, 13, 87-115,
510 10.1007/BF00002772, 1991.

511 von Caemmerer, S., and Farquhar, G. D.: Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves,
512 *Planta*, 153, 376-387, 10.1007/BF00384257, 1981.

513 Walinga, I., van der Lee, J. J., Houba, V. J. G., van Vark, W., and Novozamsky, I.: Plant analysis Manual, in, Kluwer Academic Publishers,
514 Agricultural University, Wageningen, The Netherlands, 1989.

515 Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D.,
516 and Woodward, F. I.: The relationship of leaf photosynthetic traits - Vcmax and Jmax - to leaf nitrogen, leaf phosphorus, and specific leaf
517 area: a meta-analysis and modeling study, *Ecology and Evolution*, 4, 3218-3235, 10.1002/ece3.1173, 2014.

518 Walker, T. W., and Syers, J. K.: The fate of phosphorus during pedogenesis, *Geoderma*, 15, 1-19, [https://doi.org/10.1016/0016-](https://doi.org/10.1016/0016-7061(76)90066-5)
519 [7061\(76\)90066-5](https://doi.org/10.1016/0016-7061(76)90066-5), 1976.

520 Wieder, W. R., Cleveland, C. C., Smith, W. K., and Todd-Brown, K.: Future productivity and carbon storage limited by terrestrial nutrient
521 availability, *Nature Geoscience*, 8, 441-444, 10.1038/ngeo2413, 2015.

522 Wright, S. J., Yavitt, J. B., Wurzburger, N., Turner, B. L., Tanner, E. V. J., Sayer, E. J., Santiago, L. S., Kaspari, M., Hedin, L. O., Harms,
523 K. E., Garcia, M. N., and Corre, M. D.: Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland
524 tropical forest, *Ecology*, 92, 1616-1625, 10.1890/10-1558.1, 2011.
525 Wright, S. J., Turner, B. L., Yavitt, J. B., Harms, K. E., Kaspari, M., Tanner, E. V. J., Bujan, J., Griffin, E. A., Mayor, J. R., Pasquini, S. C.,
526 Sheldrake, M., and Garcia, M. N.: Plant responses to fertilization experiments in lowland, species-rich, tropical forests, *Ecology*, 99, 1129-
527 1138, <https://doi.org/10.1002/ecy.2193>, 2018.
528 Wright, S. J.: Plant responses to nutrient addition experiments conducted in tropical forests, *Ecological Monographs*, 89, e01382,
529 <https://doi.org/10.1002/ecm.1382>, 2019.
530 Wurzburger, N., Bellenger, J. P., Kraepiel, A. M. L., and Hedin, L. O.: Molybdenum and Phosphorus Interact to Constrain Asymbiotic
531 Nitrogen Fixation in Tropical Forests, *PLOS ONE*, 7, e33710, 10.1371/journal.pone.0033710, 2012.
532 Yoda, K.: Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia, *Japanese Journal of Ecology*, 24, 247-
533 254, 10.18960/seitai.24.4_247, 1974.
534
535

536 **Tables**

537 **Table 1** Surface soil (0-15 cm) total and available nutrient concentrations measured in 2015 in the three landscape positions
 538 (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

539

540

541

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

		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

545

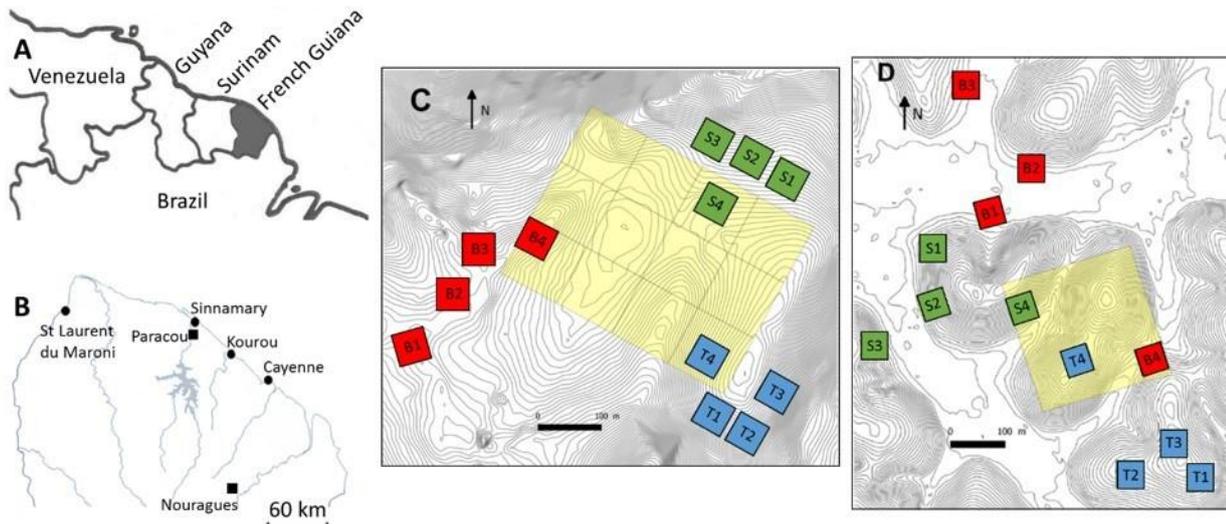
546 **Table 3 Overview of the number of *A_n-C_i* curves measured in this study. Measurements were carried out in the wet and dry season,**
 547 **at different canopy levels (U = upper canopy, sunlit leaves; L = lower canopy, shaded leaves; M = middle canopy leaves), at different**
 548 **field sites (Nouragues-Inselberg, Nouragues-Pararé, Paracou). The measurements carried out on saplings instead of on mature,**

549 canopy trees are mentioned separately. Pre-treatment measured were carried out in 2015 and 2016, whereas post-treatment (after
 550 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	
2015	141	82	146	76				61	113	56	120	
2016								42		35		38
2017					37	45	32					46
2019	156		163					155		164		

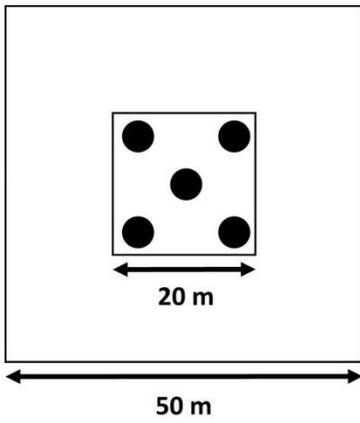
551

552 **Figures**



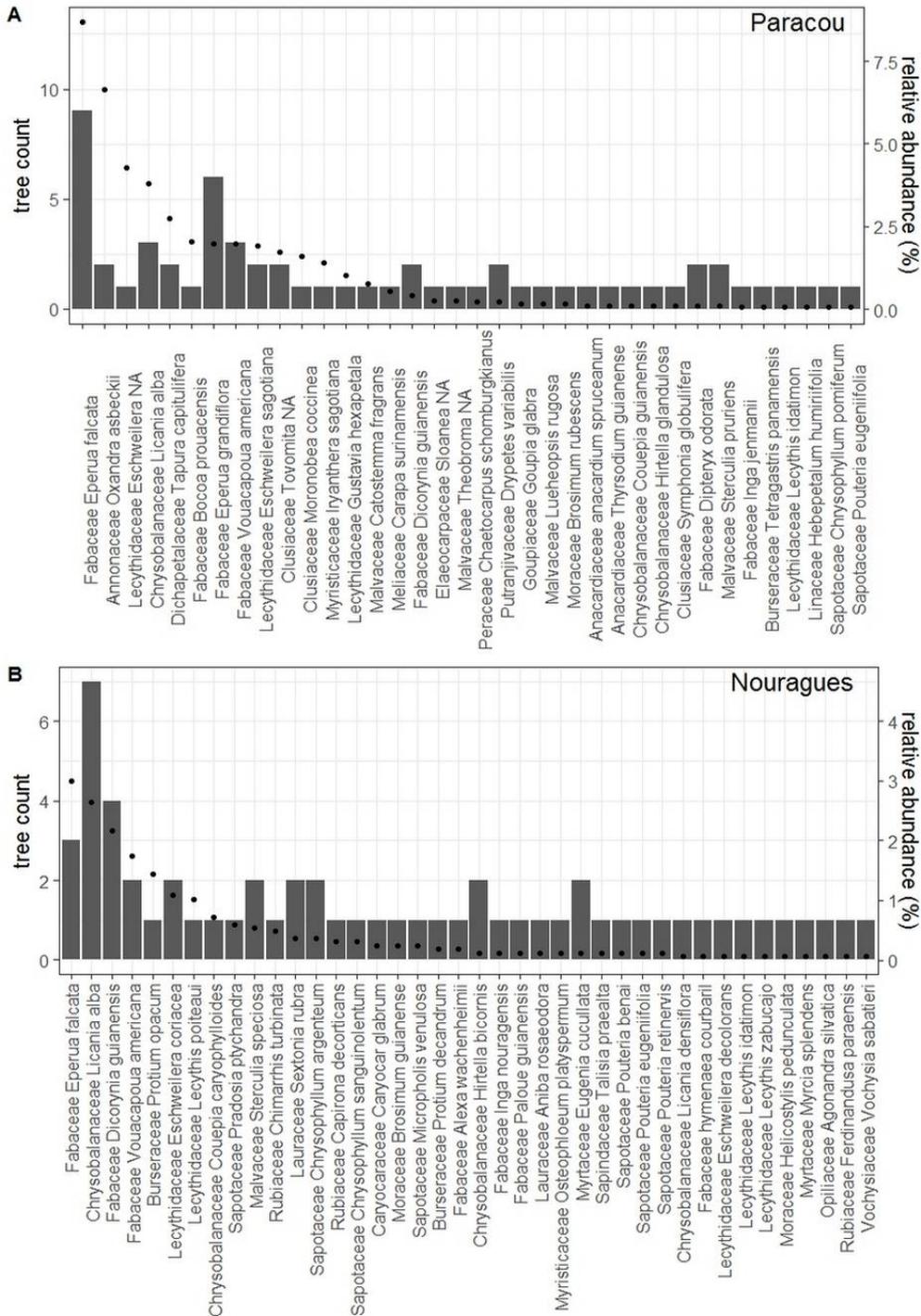
553

554 **Figure 1** Situational map: (A) north-eastern part of South America, (B) northern French Guiana with its main cities (circles) and
 555 the experimental sites Paracou and Nouragues (closed squares), (C) the twelve study 50 x 50 m plots of this study at Nouragues-
 556 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).
 557 Plots are marked by a letter describing the topography (B = bottom, S = slope, T = top) and a number describing the nutrient
 558 addition treatment (1 = +N, 2 = +NP, 3 = +P, 4 = control).



559

560 **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
561 **plots.**

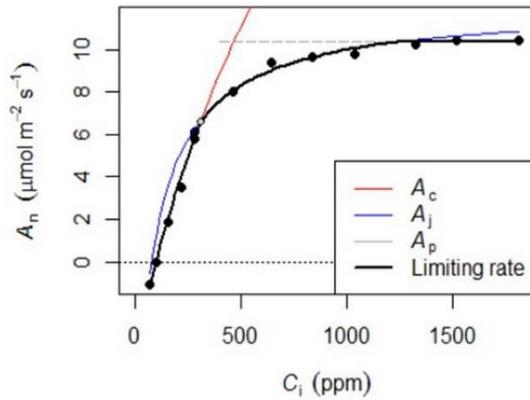


562

563 **Figure 3** Number of mature trees we sampled per species (bars) and the relative abundance for each species (dots) are shown for (A)

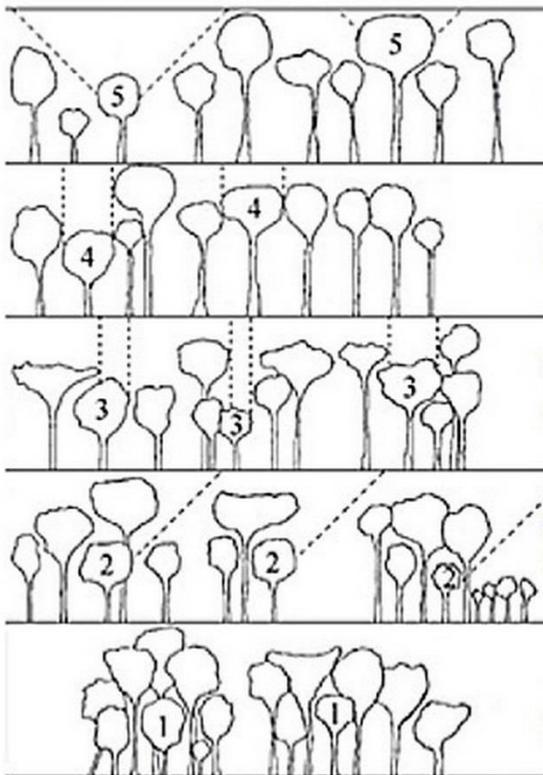
564 **Paracou** and (B) **Nouragues**. Relative abundance was calculated as the percent composition of each species relative to the total

565 **number of that species with all 50 x 50 m plots at Paracou or Nouragues.**



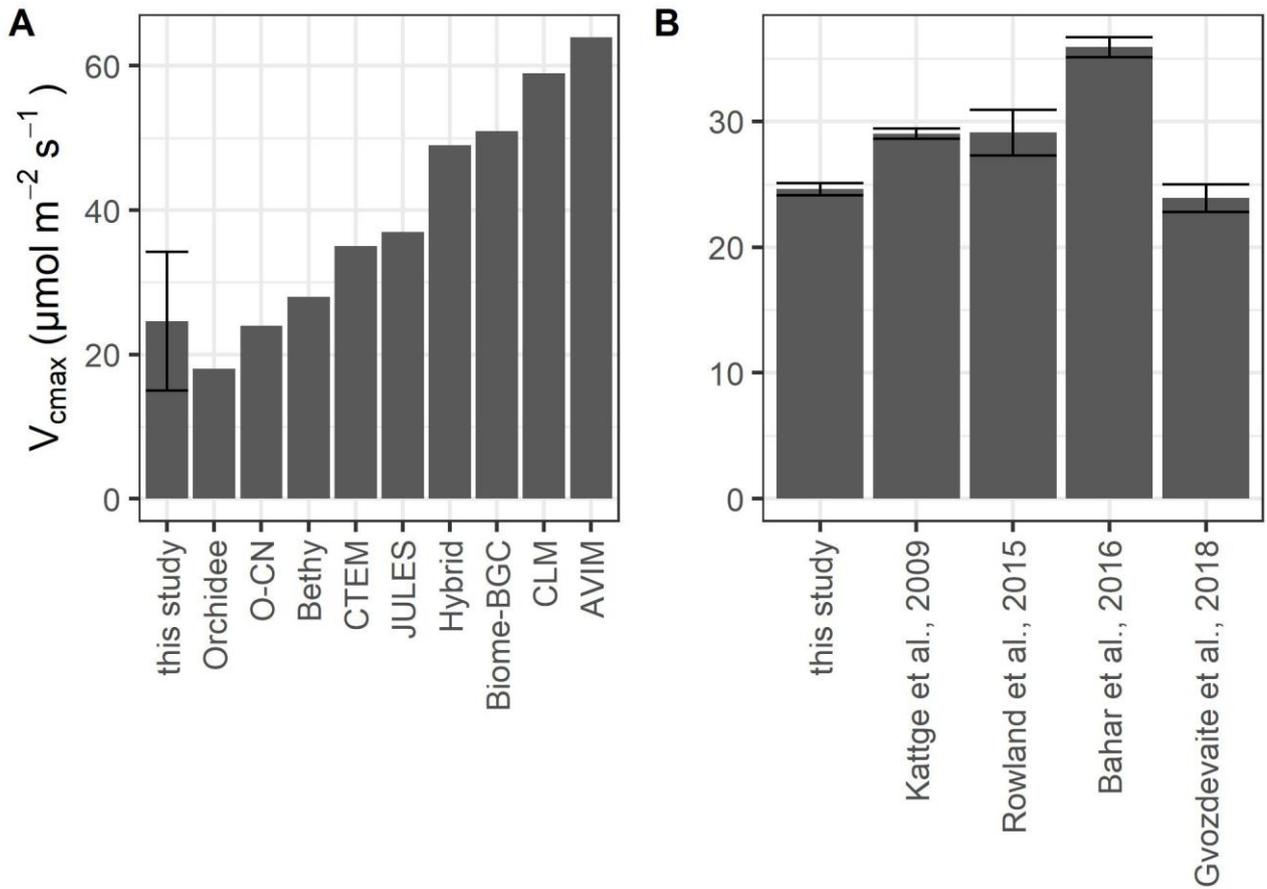
566

567 **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:
 568 rubisco (A_c), RuBp (A_j) or TPU (A_p).



569

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



574

575 **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
 576 (B) other lowland tropical sites growing on nutrient-poor oxisols. The values for the models were adopted from Rogers (2014) for the
 577 plant functional types “broadleaf evergreen tropical tree” (Orchidee, O-CN, CLM, AVIM), “tropical tree (oxisol)” (Bethy), “rainforest”
 578 (Hybrid), “evergreen broadleaf tree” (Biome-BGC, CTEM), and “broadleaf tree” (Jules). We did not include IBIS, which was also
 579 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
 580 error.