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26 **ABSTRACT**

27 Increasing soil organic carbon (SOC) in agroecosystems is necessary to mitigate climate
28 change and soil degradation. Management practices designed to reach this goal call for a
29 deeper understanding of the processes and drivers of soil carbon input stabilization. We
30 identified main drivers of SOC stabilization in oil palm plantations using the well-defined
31 spatial patterns of nutrients and litter application resulting from the usual management
32 scheme. The stabilization of oil palm-derived SOC (OP-SOC) was quantified by $\delta^{13}\text{C}$ from a
33 shift of C4 (savanna) to C3 (oil palm) vegetations. Soil organic carbon stocks under frond
34 piles were 20 and 22 % higher compared to harvest paths and interzones, respectively.
35 Fertilization and frond stacking did not influence the decomposition of savanna-derived SOC.
36 Depending on management zones, net OP-SOC stabilization equalled 16-27% of the fine root
37 biomass accumulated for 9 years. This fraction was similar between frond piles and litter-free
38 interzones, where mineral NPK fertilization is identical, indicating that carbon inputs from
39 dead fronds did not stabilize in SOC. A path analysis confirmed that the OP-SOC distribution
40 was largely explained by the distribution of oil palm fine roots, which itself depended on
41 management practices. SOC mineralization was proportional to SOC content and was
42 independent on phosphorus availability. We conclude that SOC stabilization was driven by C
43 inputs from fine roots and was independent of alteration of SOC mineralization due to
44 management. Practices favouring root growth of oil palms would increase carbon
45 sequestration in soils without necessarily relying on the limited supply of organic residues.

46

47 **KEYWORDS:** carbon isotopes - fertilization - fine roots - microbial activity - structural
48 equation modelling - savanna - Colombia

49

50 **1. INTRODUCTION**

51 Soil organic carbon (SOC) depletion in agroecosystems is a major source of greenhouse gas
52 emissions, resulting in losses of soil fertility and ecosystem stability (Amundson et al., 2015).
53 Policymakers have recently acknowledged the promotion of soil C sequestration in
54 agroecosystems as a promising strategy to simultaneously mitigate climate change and
55 enhance food security (Lal, 2016). Nonetheless, management practices favouring soil C
56 sequestration lead to highly variable outcomes, calling for a deeper understanding of
57 processes and factors controlling C stabilization, especially after land-use changes (Ghimire,
58 Lamichhane, Acharya, Bista, & Sainju, 2017; Haddaway et al., 2017). This is particularly
59 needed in regions that are undergoing rapid and substantial land degradation following
60 conversion from largely forested landscapes to intensive agricultural systems, as has been the
61 case in tropical landscapes dominated by oil palm (*Elaeis guineensis*) plantations. In Sumatra,
62 a region with a long history of oil palm cultivation, a significant proportion of oil palm
63 plantations has already reached a critical low level of SOC content (< 1%) in the topsoil
64 (Guillaume, Holtkamp, Damris, Brümmer, & Kuzyakov, 2016).

65 Stocks of SOC depend on the balance between soil C inputs from vegetation and outputs
66 from SOC mineralization, erosion and leaching (Lorenz & Lal, 2018). This balance is strongly
67 affected by the conversion of natural ecosystems to intensive agricultural land (Guillaume et
68 al., 2018). Predicting impacts of land-use change and management on SOC dynamics and its
69 stabilization faces major difficulties as many factors affect both litter input and mineralization
70 processes that determine the fraction of C input stabilized in SOC. While higher plant biomass
71 inputs might lead to higher SOC accumulation, an increase of fresh organic matter inputs may
72 enhance the mineralization of more recalcitrant SOC that ultimately reduces the gain in SOC,
73 a process known as priming (Kuzyakov, Friedel, & Stahr, 2000). Nutrient application
74 modifies the stoichiometry of organic matter inputs and of soil organic matter, which in turn

75 affects microbial processes controlling SOC stabilization (Qiao et al., 2016; Zang, Wang, &
76 Kuzyakov, 2016). For instance, altered microbial carbon use efficiency (i.e. the ratio of C
77 incorporated into microbial biomass to the added C) or mining for nutrients from recalcitrant
78 SOC result in either SOC gains or losses (Finn et al., 2016; Kirkby et al., 2014). Quantifying
79 soil C inputs remains a methodological challenge and few data are available, for instance, on
80 root turnover, rhizodeposition, and the fraction of aboveground litter C stabilized in SOC
81 (Pausch & Kuzyakov, 2018). Experimental data are especially limited for perennial plants in
82 tropics and subtropics.

83 The fast SOC turnover in the tropics makes soils particularly sensitive to land-use
84 change (Guillaume, Damris, & Kuzyakov, 2015; Pabst, Gerschlauser, Kiese, & Kuzyakov,
85 2016; Zech et al., 1997). For example, soil C inputs decrease up to 90% when rainforests are
86 converted to oil palm plantations, resulting in a rapid drop of SOC (Guillaume et al., 2018).
87 Soil organic C losses are not, however, uniform within plantations, and specific management
88 zones within the plantation may even exhibit a gain in SOC (Khasanah, van Noordwijk,
89 Ningsih, & Rahayu, 2015; Rahman et al., 2018). Soil C inputs in mature oil palm plantations
90 without cover crops (the most common practice) occurs mostly belowground through
91 rhizodeposition because the understory is frequently cleared. Significant aboveground C
92 inputs occur only under frond piles, i.e. zones where dead fronds are stacked. A gradient of
93 fertilizer application is superimposed on the gradient of soil C input: most fertilizers are
94 applied around the trunks and, in some cases, additionally to the whole surface area at lower
95 rate, including the frond piles but excluding the harvest path. These management practises
96 lead to characteristic management zones with specific factors affecting SOC dynamics (Fig
97 1a). With plantation ageing, the heterogeneity of SOC distribution increases, depending on
98 the distance to the tree, the presence of frond piles and fertilizer applications (Frazão,
99 Paustian, Pellegrino Cerri, & Cerri, 2013; Goodrick et al., 2015). Carbon and nutrients cycling

100 are, thus, highly heterogeneous leading to a variable SOC equilibrium depending on
101 management practices. This highlights the possibility to promote the increase of overall SOC
102 stocks by redesigning management practices to reach this goal.

103 In Colombia, oil palm plantations are often established on native savanna grasslands
104 dominated by grasses with a C4 photosynthesis pathway. The shift from C4 (grasses) to C3
105 vegetation (oil palm) allows source determination in soil organic matter using its $\delta^{13}\text{C}$
106 signature (Balesdent & Mariotti, 1987). The aim of the present study is to disentangle the
107 effects of soil C and nutrient inputs on newly accumulated SOC (oil palm-derived) and the
108 decomposition of old SOC (savanna-derived), taking advantage of the specific patterns of
109 fertilization and soil C inputs in the four management zones. We hypothesized that soil C
110 inputs and consequent SOC accumulation increase with fine root density, which itself depends
111 on plantation age and distance to trees, as well as on the presence of frond piles. Fertilizer
112 application is, however, expected to decrease SOC stabilization rates where soil C inputs are
113 low. Hence, the specific aims of the study are to i) quantify the new oil palm-derived (C3
114 signature) and the old savanna-derived SOC stocks (C4) in a mature oil palm plantation
115 established on native savanna grassland, ii) assess oil palm root development and its impact
116 on SOC accumulation with plantation age, iii) determine the impacts of management practices
117 on root development and soil microbial activity and iv) identify the main factors (root density,
118 nutrient availability, microbial activity) driving SOC stabilization.

119

120 **2. MATERIALS AND METHODS**

121

122 ***2.1. Study area***

123 The study was conducted in the Eastern Plains (*Llanos Orientales*), Department Meta,
124 Colombia (4°05'7.0"N, 71°53'59.0"W). The region experiences a tropical climate (mean

125 annual temperature of 26 °C and yearly precipitation of 2200 mm yr⁻¹) with a distinct dry
126 season from December to March and 95% of the yearly rain falling between April and
127 November (Lavelle et al., 2014; Rippstein, Amézquita, Escobar, & Grollier, 2001). The study
128 site lies in the slightly undulating well-drained high plains (Altillanura plana) dominated by
129 Plinthosols and Ferralsols (IUSS Working Group WRB, 2014). These soils have a low
130 fertility, high acidity and high aluminium saturation limiting agricultural production (Lavelle
131 et al., 2014; Rippstein et al., 2001). The natural vegetation is an herbaceous savanna with
132 scarce bushes, which is drained by many small rivers. Gallery forests (morichales) grow in
133 the depressions along these rivers (Rippstein et al., 2001).

134 Two unmanaged native savanna sites and three oil palm plantations with increasing age
135 (2-, 4-, and 9-year old) were selected within an area of approximately 8 × 8 km and sampled
136 in July and August 2016 (Fig. S1). Sites were carefully chosen with the help of plantation
137 agronomists to ensure that the investigated plantations had been established on unmanaged
138 native savannas, i.e. no cattle grazing in the past. Soils in the five selected sites were classified
139 as sandy-loam Ferralsols (clay content and pH ranging from 11 to 16% and from 4.5 to 5.3 in
140 the top 30 cm, respectively) with compacted top soil (bulk density ranging from 1.31 to 1.46
141 g cm⁻³ in the top 10 cm). Drivers of SOC stabilization were assessed in the 9-year old
142 plantation. The 2- and 4-year old plantations were selected to assess the development of oil
143 palm rooting system and its relationship with SOC accumulation.

144

145 ***2.2. Plantation management***

146 Oil palm plantations had been established on native savannas whose soils were first loosened
147 with a chisel plough (to a depth of 40 cm) and tilled with an overturning plough (10 cm).
148 Liming and phosphate rocks were applied before planting palms. Oil palm trees had been
149 planted in a triangular grid pattern with a distance of 9 m between trees, leading to 143 palms

150 ha⁻¹ (Fig. 1b). In the young plantations (2- and 4-year old), a mixture of Kudzu (*Pueraria*
151 *phaseoloides*) and Desmodium (*Desmodium heterocarpon* subsp. *ovalifolium*) cover crops
152 (C3 vegetation) have been implemented after planting. Cover crops were never used in the
153 mature plantation (9 years), and in this case the soil was always kept bare after planting with
154 oil palms. Accordingly, C3-derived SOC in the 9-year old plantation are attributed solely to
155 oil palm-derived SOC.

156 Oil palm management leads to four well-defined management zones in productive
157 plantations (about 4 years after establishment). In the study region, the weeded circle (WC)
158 around the oil palm trunk is always kept free of vegetation (Fig. 1). At young ages (2- and 4-
159 year old), all fertilizers are applied in WC. Associated with the beginning of harvest after 4
160 years, pruning starts and fronds are piled up in between palm trees (frond pile, FP). Each
161 second avenue between palm lines becomes a harvest path (HP), where machines circulate.
162 In productive plantations (after 4 years), fertilizers are evenly spread from the harvest path by
163 machines, i.e. all management zone receive the same amount of fertilizers except the harvest
164 path that receive none. The remaining area, especially the alternating avenue, represents the
165 fourth zone, where the soil is kept bare and fertilization starts after 4 years (interzone, IZ).
166 The relative surface area of the four management zones were 60% (IZ), 18% (HP), 12% (WC)
167 and 10% (FP). Fertilization depends on oil palm stand age. The 9-year old plantation received
168 per hectare during the first year about 240 kg of NPK, 60 kg of kieserite (MgSO₄), and 25 kg
169 of KCl, of zinc and of boron. The amount of NPK increased over time while the use of other
170 types of fertilizer varied from year to year. The year before sampling, 600 kg of NPK, 200 kg
171 of phosphate rocks and 160 kg of KCl-MgO per hectare were spread in the plantation.

172

173 **2.3. Soil and roots sampling**

174 Plots of 1 ha were established in all plantations and savannas in areas with homogeneous soil,
175 far from the influence of roads, rivers or groundwater, free of laterite formations (arecife) and
176 without former amendment of compost or residues from processing oil mills. Five trees as
177 replicates for management zones were selected randomly in each plantation. For each of the
178 five replicate of trees, the adjacent management zones (FP, HP, IZ, and WC) were sampled
179 on a systematic grid (Fig. 1). Frond piles, harvest paths and interzones were sampled at the
180 same distance from trees (4.5 m) to assess the effects of management starting 4 years after
181 establishment. Two additional points in the interzone were sampled at 2 and 3 m away from
182 the trunk to assess the horizontal expansion of oil palm roots (IZ2, IZ3, Fig. 1). In the 2- and
183 4-year old plantations, only the weeded circles and interzones were sampled because of the
184 absence of frond piles and harvest path in young plantations. In the 2-year old plantation, the
185 point IZ3 was not sampled, as root densities were already low in IZ2 (Fig. S2). In the savanna
186 plots, five sampling points were selected at regular distances along a 100 m transect.

187 Roots and soils were sampled with a cylindrical corer of 5 cm diameter at three depth
188 intervals (0-10, 10-20 and 20-30 cm). Roots were separated from soil by sieving at 2 mm and
189 rinsed to remove attached mineral particles. Fine roots that passed through the sieve were
190 manually picked. For the 2- and 4-year old plantations outside of weeded circles, cover crop
191 roots were removed from oil palm roots. Oil palm roots were divided into coarse roots (> 2
192 mm, corresponding to primary and secondary roots of oil palms) and fine roots (< 2 mm,
193 corresponding to tertiary and quaternary roots of oil palms). Dry root biomass was determined
194 after drying at 60 °C for 48 h. Soil samples were air-dried and sieved at 2 mm directly after
195 collection and further oven dried at 40 °C for 48 h prior to laboratory analyses.

196

197 **2.4. Soil analysis**

198 Total C and nitrogen (N) contents in soil, as well as $\delta^{13}\text{C}$ signature were determined at the
199 University of Göttingen with an isotope ratio mass spectrometer (Delta Plus, Finnigan MAT,
200 Bremen, Germany). Because of the absence of carbonates in acidic soils, total C represents
201 organic C. Residual water content was assessed by drying soil samples at 105 °C for 24 h.
202 Bulk density was measured by inserting horizontally two cylinders of 100 cm³ per depth at 0-
203 5, 5-10, 10-20 and 20-30 cm depth in a soil pit located at the centre of each sampling plot.
204 Bulk density in each cylinder was determined after drying at 105 °C and averaged between
205 four cylinders for 0-10 cm depth interval and 2 cylinders for 10-20 and 20-30 cm depth
206 intervals. Carbon stocks were calculated multiplying C contents with bulk density and the
207 layer thickness and the respective fractions of C4 (savanna-derived C) and C3 (oil palm-
208 derived) SOC. Soil available phosphorous (P) was determined using Bray II extraction
209 method (Bray & Kurtz, 1945). Three grams of soil were extracted by shaking for 15 min with
210 20 ml of 0.03 N NH₄F and 0.025 N HCl. Filtered extracts were mixed with a colorimetric
211 reagent ((NH₄)₆Mo₇O₂₄ – SnCl₂) and absorbance was measured with a UV/VIS spectrometer
212 at 660 nm (Lambda 35, Perkin Elmer, Buckinghamshire, United Kingdom).

213

214 **2.5. C3 and C4 derived carbon**

215 Relative portion of oil palm- and savanna-derived C in SOC were calculated based on the
216 differences in $\delta^{13}\text{C}$ signature of biomass between savanna grassland, dominated by C4
217 photosynthetic pathway, and oil palms, C3 photosynthetic pathway, using two sources linear
218 isotopic mixing model (Balesdent & Mariotti, 1987):

$$219 \quad f_{OP_d} = \frac{\delta^{13}\text{C}_{S_d} - \delta^{13}\text{C}_{NS_d}}{\delta^{13}\text{C}_{OP_b} - \delta^{13}\text{C}_{NS_b}}$$

220 where f_{OP_d} is the fraction of oil palm (C3)-derived SOC, $\delta^{13}\text{C}_{S_d}$ is the isotopic signature
221 measured in a soil sample at depth d, $\delta^{13}\text{C}_{NS_d}$ is the average isotopic signature at the

222 corresponding depth in natural savanna reference sites, $\delta^{13}\text{C}_{\text{OP}_b}$ is the averaged signature of
223 oil palm fine roots in the mature oil palm plantation (mean = -28.2‰, standard deviation (SD)
224 = 0.18, n = 9) and $\delta^{13}\text{C}_{\text{NS}_b}$ is the average isotopic signature of the aboveground and
225 belowground savanna biomass determined on representative subsamples of aboveground
226 biomass collected on 1 m² and fine roots collected with soil cores at each sampling point
227 (mean = -13.6 ‰, SD = 1.1, n = 19). This approach assumes that the ¹³C fractionation
228 occurring during the integration of biomass into SOC at each soil depth is the same for
229 savanna and oil palm biomass (Pausch & Kuzyakov, 2012). No ¹³C fractionation was
230 observed between savanna plant biomass and savanna SOC in 0-10 cm layer (-13.7 ‰, SD =
231 0.5, n = 10).

232

233 ***2.6. Carbon stabilization per cumulative standing root biomass***

234 Fine root stocks served as a proxy for the C input from oil palm roots. To account for
235 differences in root stocks between management zones and root development time depending
236 on the distance to the palm tree, cumulative standing fine root biomass in each management
237 zone was estimated by fitting a linear model on root biomass measured in various plantation
238 ages. The model was integrated starting from plantation establishment for WC, but only
239 starting from 4 years for IZ, FP and HP, i.e. when oil palm rooting system reached 4.5 m away
240 from the tree (Fig. S2). Assuming constant belowground C input per unit of fine roots (Pausch,
241 Tian, Riederer, & Kuzyakov, 2013), oil palm-derived SOC stocks were normalized per unit
242 of cumulated fine root biomass to assess the effect of management zones on net C3
243 stabilization efficiency.

244

245 ***2.7. Soil incubation***

246 Microbial biomass was analysed after incubation of topsoils (0-10 cm) from the 9-year old
247 plantation (zones FP, HP, IZ and WC). Twenty grams of dry soil were rewetted to 60% WHC
248 and incubated at 25 °C for 31 days. Jars were ventilated and weighed every week and rewetted
249 once to compensate for the evaporated water. Carbon and nitrogen (N) in microbial biomass
250 were measured at the end of the incubation by the fumigation-extraction method (Vance et
251 al., 1987). For C and N contents, 5 g of incubated soil were fumigated for 24 h with ethanol-
252 free CHCl₃ in a desiccator. Soils were extracted by shaking 1 h in 25 ml solution of 0.5 M
253 K₂SO₄ and then filtered. Non-fumigated samples were processed in parallel. Total extractable
254 organic C and N were analysed with a TOC-N analyser (Shimadzu, Kyoto, Japan). Extractable
255 C in the non-fumigated samples was assumed to represent dissolved organic carbon (DOC).
256 Microbial biomass C and N were calculated as the difference between fumigated and non-
257 fumigated samples, which were used also to calculate microbial C:N ratio. Microbial biomass
258 C was corrected by dividing extractable C with a factor of 0.45 (Beck et al., 1997), N with a
259 factor of 0.54 (Brookes, Landman, Pruden, & Jenkinson, 1985).

260

261 **2.8. Basal respiration**

262 Basal respiration of the rewetted samples was measured with the MicroResp™ kit (Campbell,
263 Chapman, Cameron, Davidson, & Potts, 2003). Three analytical replicates of 0.5 g for each
264 field replicate were taken from the incubation jars after rewetting and incubated in 96 deep-
265 well plate in parallel to the incubation in jars. Soil was kept moist by a moist paper towel
266 fixed on the plate. Respiration was measured 1, 2, 4, 8, 15, 18, 24 and 31 days after rewetting
267 using a MicroResp™ kit (Campbell et al., 2003). To remove residual CO₂ in the wells, the
268 plate was aerated with a fan before incubating for 6 h with the indicator plate on top (at 27
269 °C). The indicator plate was read before and after incubation with a spectrophotometer
270 (Microplate reader BioTek SynergyMX) at 570 nm. Absorption calibration was done by

271 dissolving a known amount of NaCO₃ with 1 M HCl in excess in closed jars with eight
272 microwells of the indicator plate for 6 h (Campbell et al., 2003).

273 Soil respiration was partitioned using a two-pool mixed-model to describe SOC
274 mineralization kinetics (Bonde & Lindberg, 1988). The first pool follows a first-order
275 decomposition kinetics, while the second follows a zero-order kinetics, corresponding to the
276 stabilized basal respiration:

$$277 \quad C_{min} = C_l(1 - e^{-tk_l}) + BR t$$

278 where t is the time, C_{min} is the cumulative CO₂ mineralized to time t , C_l is the labile C pool
279 released from sample preparation and re-wetting, k_l is the decomposition constant of the labile
280 pool and BR is the basal respiration. The basal respiration of each field replicate was
281 determined by fitting the model on the three analytical replicates. The metabolic quotient is
282 the ratio of basal respiration over microbial biomass C (C_{mic}).

283

284 **2.9. Statistical analyses**

285 All statistical analyses were performed using the open source software R version 3.2.1 (R
286 Core Team, 2016). One sampling point in WC and one in IZ were removed from all analyses
287 due to very low $\delta^{13}C$ signatures, probably resulting from the former presence of C3 bush at
288 these exact sampling locations. We used a linear mixed-effects model approach (“lme4”
289 package), followed by Tukey HSD tests for post hoc pairwise comparisons, to test for the
290 effects of management zones (FP, HP, IZ and WC) on soil parameters (bulk, C3 and C4
291 stocks, fine root biomass, net C3 stabilization, basal respiration, microbial biomass C and C:N
292 ratio, and metabolic quotient) at each soil depth (0-10, 10-20 and 20-30 cm) in the mature
293 plantation (9-year old) with palm trees as random factor. Normal distribution of residuals and
294 homogeneity of variance were tested by Shapiro and Levene tests, respectively, and data was
295 log-transformed if necessary. Causal relationships between parameters (C stocks vs. age, C3

296 stocks vs. fine roots) were assessed by linear regressions. Average C stocks at plot scale down
297 to 30 cm depth were calculated using the relative surface area of each management zone.
298 Associations among parameters were calculated using Pearson correlation. *P-values* were
299 determined using the function *cor.test*.

300 A path analysis was performed to disentangle the direct and indirect effects of fine roots,
301 soil microorganisms and nutrient application on the accumulation of oil palm-derived SOC
302 by using the “lavaan” package (Rosseel, 2012). Based on the priori knowledge, we developed
303 an initial conceptual model that was both consistent with our data and which made biological
304 sense (Fig. S3). We first created five conceptual groups of measured variables, which
305 represented i) nutrient application (measure of available P), ii) fine roots C inputs (measure
306 of fine roots biomass), iii) SOM quality (measure of C:N ratio of SOM), iv) SOC
307 accumulation (measure of oil palm-derived SOC) and v) soil microorganism effects. As a
308 proxy for the microbial effect, we used the score of each sample on the first axis (PC1 = 68
309 %) of a principal component analysis (PCA) including all microbial related variables (soil
310 basal respiration, metabolic quotient, Nmic, Cmic, microbial C:N ratio) (Fig. S4). The
311 conceptual model hypothesized that fine roots biomass and microbial activity have a direct
312 impact on oil-palm SOC accumulation. Both might be affected by nutrient application.
313 Additionally, microbial activity would be directly affected by root density through the amount
314 of rhizodeposition and indirectly by changing organic matter quality. Finally, P availability
315 could have a direct effect on microorganisms and SOM quality by changing the resources’
316 stoichiometry in the soil. Pedoclimatic factors affecting SOC stabilization (e.g. soil
317 mineralogy) were not specified in the model because they are identical between zones and
318 cannot be modified by management. The adequacy of the model was determined by non-
319 significant differences between the predicted and observed covariance matrices (χ^2 tests, $p >$
320 0.05), low root mean squared error of approximation index (RMSEA < 0.1), high Tucker-

321 Lewis index (TLI > 0.90) and high comparative fit index (CFI > 0.90) (Grace, 2006; Rosseel,
322 2012).

323

324 **3. RESULTS**

325

326 ***3.1. Soil organic carbon stocks and origin***

327 Observations done on the 9-year old plantation showed lower soil C stocks compared to the
328 native savanna grasslands (Fig. 2). On average, 1.0 ± 0.2 kg C m⁻² was lost down to 30 cm
329 depth, considering the relative area of each management zone. However, spatial SOC
330 distribution in the mature oil palm plantation depended on management zones. Soil C losses
331 during that period of time in the top 10 cm under frond piles and, to a lesser extent, under
332 weeded circles were lower than C losses in harvest paths and interzones (Fig. 2). This trend
333 was similar down to 30 cm depth but the differences were not significant below 10 cm depth.
334 Differences in SOC stocks between management zones arose mainly from a higher
335 accumulation of oil palm-derived SOC (C3-derived) under frond piles and weeded circles
336 (Fig. 2). Oil palm-derived SOC after 9 years already accounted for between 27% (IZ) and
337 45% (FP and WC) of the total SOC stock in the top 10 cm, where differences between zones
338 were highest. Below 20 cm depth, the contribution of oil palm-derived SOC dropped,
339 accounting for 2% (IZ) and maximum 12% (WC) of the total SOC stocks. The amount of
340 savanna-derived SOC (C4-derived) remaining after 9 years was lower in the top 10 cm than
341 between 10-20 cm depth, indicating a faster decomposition of this C pool in the top soil
342 compared to deeper soil layers. Nonetheless, management zones had little influence on the
343 decomposition rates of savanna-derived SOC, except in 10-20 cm depth under weeded circles
344 where more C was lost than under frond piles. A similar trend was observed in the top 10 cm
345 that explains why total SOC under weeded circles was intermediate as compared to frond

346 piles and harvest paths, despite the high amount of oil palm-derived SOC stabilized under
347 weeded circles.

348

349 **3.2. Root development and C inputs**

350 Oil palm fine roots were first observed at 4.5 m away from palm trees in two out of the five
351 investigated palms in the 4-year old plantations (Fig. S2). This indicates that oil palm rooting
352 systems from adjacent palms started to overlap at that age, but root biomass at 4.5 m was still
353 very low. Fine root biomass under weeded circles increased constantly during 9 years (Fig.
354 3a). At the age of 9 years, roots were observed in all management zones but root growth was
355 strongly enhanced under frond piles, reaching the same fine root biomass as under weeded
356 circles in only 5 years, well above fine root biomass in the interzones and harvest paths (Fig.
357 3a).

358 Oil palm-derived SOC under weeded circles was highly correlated with fine root
359 biomass (Fig. 3b). Oil palm-derived SOC stocks corresponded to 70 ± 5 % of fine root
360 biomass stocks (slope = 0.70, $R^2 = 0.80$) at the time of measurement, independently of soil
361 depth and plantation age. This percentage was relatively constant between the three soil
362 depths; from 62 ± 10 % in the top 10 cm to 50 ± 11 % between 20-30 cm depth (Table 1). Oil
363 palm-derived SOC accumulation per year was 3 to 4 times faster in the top soil 10 cm than in
364 the underlying layers (Table 1).

365 While oil palm-derived SOC in the weeded circle was accumulating from the beginning
366 of the plantation, root biomass was measured at fixed time points. Oil palm fine root biomass
367 was integrated over the whole duration of the plantation to calculate the cumulative fine roots
368 biomass for each year and soil depth under weeded circles. Accordingly, oil palm-derived
369 SOC accumulation corresponded to 14 ± 2 %, 11 ± 2 % and 11 ± 1 % of the cumulated fine roots
370 biomass stocks under weeded circles at 0-10, 10-20 and 20-30 cm depth, respectively (Table

371 1). Since soil depth had little impact on the relationship between oil palm-derived SOC and
372 fine root biomass, differences in oil palm-derived SOC stabilization rates between depths
373 were mainly related to differences in fine root biomass. The linear relationship across age
374 showed that the proportion of oil-palm derived SOC stabilizing per amount of fine roots
375 present in the plantation remains constant at least during 9 years (Fig. 3b).

376 Oil palm derived-SOC and fine root biomass were similar under frond piles and weeded
377 circles in the top 10 cm in the 9-year old plantation (Fig. 3a). However, fine roots appeared
378 at 4.5 m away from palms 4 years later than under weeded circles. To remove the effects of
379 root density and duration of C inputs between zones, oil palm-derived SOC stocks were also
380 divided by the cumulative roots biomass stocks and compared between management zones
381 (Fig. 4).

382 After this normalization to the amount of fine root biomass, the stabilization of oil palm-
383 derived SOC was similar between frond piles and interzones, two zones receiving the same
384 amount of mineral fertilizers and sampled at the same distance to the tree. Consequently, only
385 little C from the large amount of C present in dead fronds is eventually stabilized in SOC. The
386 stabilization of oil palm-derived SOC was lower under weeded circles, the zone receiving the
387 largest amount of mineral fertilizer, than under harvest paths, the only zone experiencing no
388 direct application of mineral fertilizers.

389

390 ***3.3. Soil microorganisms and fertility***

391 Microbial activity (basal respiration and metabolic quotient) and biomass (microbial biomass
392 C and microbial C:N ratio) parameters were similar under frond piles and weeded circles (Fig.
393 5). In these two zones, the same amount of microbial biomass respired more C compared to
394 harvest paths and interzones. Consequently, the metabolic quotient was highest under frond
395 piles and weeded circles.

396 Available P (Bray II) was an order of magnitude higher in weeded circles compared to
397 the other zones, as expected by the higher fertilization application in that zone. Weeded circles
398 also had the lowest amount of K₂SO₄-extractable C (DOC) despite high SOC content. (Table
399 S1). Between the three zones (HP, IZ and FP) located at the same distance to the palm trees
400 but varying in their management, P availability was two times lower in harvest paths ($11.1 \pm$
401 $0.3 \mu\text{g g}^{-1}$) as compared to frond piles, but well above the P availability in native savanna sites
402 ($2.2 \pm 0.3 \mu\text{g g}^{-1}$), despite the absence of direct fertilization. The DOC amount was similar
403 between the three zones and the C:N ratio was 1 unit higher under frond piles, indicating that
404 only small change in SOC quality occurred between management zones.

405

406 ***3.4. Drivers of the accumulation of oil palm-derived SOC***

407 In the three zones located at the same distance to the palm trees (HP, IZ and FP), oil palm-
408 derived SOC stocks (C₃) were highly correlated with fine root biomass ($r = 0.82$), as well as
409 to most microbial parameters, the amount of soil organic matter (C and N contents) and
410 available P (Fig. 6). The basal respiration, the metabolic quotient and the microbial biomass
411 N increased with higher oil palm-derived SOC but not with total C content, underlying the
412 role of fresh organic C to maintain microbial activity. By contrast, higher C:N ratio in
413 microbial biomass and, to a lesser extent, higher microbial biomass were associated to less
414 oil palm-derived SOC and less fine roots biomass but with more savanna-derived SOC
415 remaining after conversion to oil palm.

416 A path analysis was performed to disentangle the direct and indirect effects of fine roots,
417 soil microorganisms and nutrient availability on the accumulation of oil palm-derived SOC
418 at 4.5 m away from palm trees in the 9-year old plantation. Because of the high association
419 among all microbial parameters (Fig. 6), the scores of each sample on the first axis (PC1 = 68
420 %) of a principal component analysis (PCA) including all microbial related parameters were

421 used as a proxy for soil microorganisms in the path analysis (Fig. S4). The fitting parameters
422 of the model were good ($P\chi^2 = 0.33$, RMSEA = 0.09, TLI = 0.97, CFI = 0.99), and the model
423 explained 71% of the variance in oil palm-derived SOC (Fig. 7). Fine root biomass was
424 strongly influenced by nutrient availability (available P) and was an important driver of
425 microbial properties (i.e. increase in microbial biomass N, basal respiration, specific
426 respiration and metabolic quotient and, in the opposite, decrease of microbial biomass C and
427 C:N ratio – see also Fig. 6). By contrast, nutrient availability had only a marginal ($p = 0.09$)
428 and opposite effect on soil microorganisms. While fine root biomass influenced SOM quality
429 (C:N ratio), microorganisms were not affected by SOM quality. The direct effect of fine roots
430 on oil palm-derived SOC stabilization was 2.8 times stronger than the marginal effect ($p =$
431 0.06) of soil microorganisms. Accordingly, nutrient availability had an important indirect
432 impact on the accumulation of oil palm-derived SOC by favouring root development and
433 thereby C inputs without enhancing SOC mineralization.

434

435 **4. DISCUSSION**

436

437 ***4.1. Drivers of SOC stabilization***

438 Soil organic C stocks strongly varied depending on the management zones of the plantation.
439 Specific management impacted the amount of new oil palm C input and its stabilization into
440 SOC but had little effect on the decomposition rate of old savanna-derived SOC (Fig. 2).
441 Carbon stabilization was mainly driven by C inputs from fine roots rather than by changes in
442 C outputs from microbial mineralization (Fig. 7). The relationship between fine roots and oil
443 palm derived SOC remained weakly affected by soil depth, plantation age and management
444 zones (Table 1, Fig. 3 and 4). Fine root biomass was a good proxy for soil belowground C
445 inputs. Oil palm fine roots absorb nutrient and water, and therefore have definite growth and

446 short-term self-pruning. In contrast, coarse roots, which have the function of conduction, have
447 indefinite growth and long term self-pruning (Jourdan, Michaux-Ferrière, & Perbal, 2000;
448 Jourdan & Rey, 1997). The relationship between cumulated fine root biomass and oil-palm
449 derived SOC stocks would not remain constant once stocks reach equilibrium. The
450 relationship, however, was linear (Fig. 3), indicating that SOC stocks were still far from
451 equilibrium after 9 years of cultivation and that oil palm-derived SOC will continue to
452 increase.

453 Microbial metabolism and biomass were strongly affected by fine roots. Higher organic
454 C availability in terms of oil palm-derived SOC and C inputs under frond piles and in the
455 weeded circle were associated with microbial communities characterized by a high
456 mineralization activity but of low efficiency – the so termed *r* strategy (Loeppmann,
457 Blagodatskaya, Pausch, & Kuzyakov, 2016). The high metabolic quotient results from either
458 a low C use efficiency or a high microbial biomass turnover. By contrast, zones with low C
459 availability such as the harvest path and the interzones were associated with microbial
460 communities more efficient to maintain their biomass despite lower mineralization rates.
461 Their lower metabolic quotients and their higher C:N ratios suggest that the scarcity of C
462 increased the proportion of K strategists and fungi within microbial communities (Mouginot
463 et al., 2014; Six, Frey, Thiet, & Batten, 2006). While the main effect of nutrient availability
464 on microbial communities was indirect by increasing roots C inputs, it tended to have also a
465 minor direct but contrasting effect on microbial communities. Lower C to nutrients ratio
466 favours high C use efficiency of microorganisms, which would explain the larger microbial
467 biomass in interzones despite the low microbial activity and root density (Sinsabaugh,
468 Manzoni, Moorhead, & Richter, 2013). Nonetheless, management impacts on microbial
469 communities and their resource consumption strategies levelled-off resulting in similar
470 fraction of SOC mineralized in all management zones. Weeded circles were the only area of

471 the plantation showing slightly lower net SOC stabilization and savanna-derived SOC stocks
472 (Fig. 2 and 4). The very high amount of fertilizer applied already in the early stage of the
473 plantation might have slightly fastened SOC turnover. Nonetheless, management effects were
474 small in regards to the 10-fold increase of P availability in this zone as compared to the rest
475 of the plantation. The fact that nutrient availability had little impact on the SOC mineralization
476 and stabilization indicates that microorganisms were mostly C-limited. Indeed, soils were
477 depleted in SOC and the whole surface area of the plantations, even areas not directly
478 fertilized, experienced an increase in P availability as compared to native savannas.

479 In summary, management and its impact on soil belowground C inputs and nutrient
480 availability did not lead to priming of recalcitrant SOC nor to faster turnover of fresh organic
481 SOC, except around palms in the weeded circles. Hence, SOC distribution was not driven by
482 an altered decomposition of SOC pools but by different rates of fine root growth and the
483 resulting soil C inputs depending on management.

484

485 ***4.2. Drivers of soil C inputs***

486 Oil palm rooting system follows a relatively rigid and genetically determined development
487 (Jourdan et al., 2000; Jourdan & Rey, 1997). Primary lateral roots start to grow one year after
488 germination at a rate of 3 mm d⁻¹, confirming that roots of palms, which are planted a year
489 after germination, reach 4.5 m in the fourth year of a plantation (Jourdan & Rey, 1997).
490 Nevertheless, root development showed plasticity, reacting to management as shown by the
491 fast development of fine roots under frond piles. Root development is generally enhanced in
492 nutrients-rich zones (Hodge, 2004). Phosphorous availability was an important driver of root
493 development, favoring soil C inputs from fine roots, and consequently the accumulation of
494 new SOC (Fig. 7). Its distribution did not exactly reflect the pattern of fertilizer application
495 (Table S1). Despite no direct fertilization applications, harvest paths were enriched in

496 available P as compared to the reference savanna sites and only frond piles exhibited a
497 significantly higher P availability. This discrepancy may result from the initial soil
498 preparation with dolomite and phosphate rocks and seems to be maintained over time by the
499 recycling of organic P inputs from rhizodeposition, root turnover, and frond mineralization.
500 The positive impact of frond piles on root development is likely not limited to P availability.
501 Fronds piles increase the availability of major cations (Law, Husni, Ahmed, & Haniff Harun,
502 2009). Similarly, it was shown that the application of empty fruit bunches on the surface
503 increases soil moisture (Tao, Slade, Willis, Caliman, & Snaddon, 2016) and roots
504 development (Kheong, Rahman, Musa, & Hussein, 2010). The positive impact of frond piles
505 on SOC stocks has been previously reported (Haron, Brookes, Anderson, & Zakaria, 1998;
506 Law et al., 2009) but authors have already highlighted the small increase of SOC stocks given
507 the huge amount of frond's biomass C concentrated on a small surface area ($2-3 \text{ kg C m}^{-2} \text{ yr}^{-1}$
508 ¹ in frond piles). It was suggested that fronds were mineralized mostly aboveground with little
509 contribution to SOC (Haron et al., 1998). Our findings confirm this hypothesis and indicate
510 that the positive impacts of frond piles arise more from the improvement of soil conditions
511 (likely nutrient availability, humidity, protection from erosion) that favours root growth than
512 from their role as a C source.

513

514 ***4.3. Increasing SOC stocks***

515 Soil organic C stabilization depends on belowground C inputs and not on the management
516 induced variation of SOC mineralization rates (Fig. 7). This field evidence-based finding is
517 similar to the conclusion of a modelling study on arable cropping system in temperate zones
518 (Autret et al., 2016). Soil C inputs should be enhanced to increase soil C sequestration in oil
519 palm plantations. The current management practice that consist in piling dead fronds,
520 however, is not efficient to integrate the fronds' organic matter into the soil. This can be

521 explained by several mechanisms. First, organic matter quality in fronds is low due to high C
522 to nutrient ratios (Yusuyin et al., 2015). This decreases the C use efficiency of
523 microorganisms. Second, bioturbation from soil fauna is limited as indicated by a sharp
524 transition between decomposing fronds and the soil surface observed in the field. Soil fauna
525 abundance, especially of earthworms, and biogenic macroaggregates are lower in oil palm
526 plantations as compared to native savanna and in improved pastures (Lavelle et al., 2014).
527 Consequently, fronds' organic matter does not benefit from the protection mechanisms that
528 minerals would provide if it was integrated into the soils by fauna activity (Schmidt et al.,
529 2011). Application of composted mill residues would be a solution to decrease C to nutrient
530 ratios of litter and improve the integration of organic matter into the soil by favouring soil
531 fauna activity, humification and mineral protection.

532 The availability of organic residues from the palm oil production chain that could be
533 applied in plantations, however, is limited. Leguminous cover crops, as already implemented
534 in the younger plantations, are an alternative to increase aboveground and belowground C and
535 N inputs. Enhancing root growth by mimicking the effects of frond piles is a promising
536 solution to increase SOC if palms have plasticity to allocate more C to their rooting system
537 when soil conditions are favourable or if palm varieties are developed for that purpose. Oil
538 palm fronds could be spread on larger surface area or mixed with other residues, such as
539 empty fruit bunched or fibers, to make a mulch. Even solutions not based on organic matter
540 that would limit soil evaporation, retain nutrients, limit run-offs and erosion might improve
541 root development. Future research should address whether SOC stocks eventually recover to
542 initial SOC levels. Ensuring long-term soil fertility in oil palm plantations is fundamental to
543 avoid a conversion of natural ecosystem constrained by soil degradation in older plantation.
544 The benefits from increasing SOC in terms of climate change mitigation would cascade far
545 beyond the amount of C sequestered in the soil because of the gain in soil fertility.

546

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553

554 **CONFLICT OF INTEREST STATEMENT**

555 The authors declare no conflict of interest.

556

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721 **TABLES**

722

723 **Table 1.** Oil palm-derived SOC stabilization under weeded circles at each depth depending
 724 on time, fine root biomass in the plantation and fine root biomass cumulated since plantation
 725 establishment (mean \pm SE). All linear regressions were significant at $p < 0.001$.

726

Weeded circles Depths <i>cm</i>	OP-derived SOC per year		OP-derived SOC per fine roots		OP-derived SOC per cumulative fine roots	
	<i>g SOC m⁻² yr⁻¹</i>	<i>R²</i>	<i>g SOC g⁻¹ roots</i>	<i>R²</i>	<i>g SOC g⁻¹ roots</i>	<i>R²</i>
	0-10 (n=14)	54 \pm 6	0.85	0.62 \pm 0.10	0.76	0.14 \pm 0.02
10-20 (n=15)	18 \pm 6	0.55	0.53 \pm 0.11	0.60	0.11 \pm 0.02	0.59
20-30 (n=15)	12 \pm 2	0.75	0.50 \pm 0.11	0.57	0.11 \pm 0.01	0.80

727

728

729 **FIGURE LEGENDS**

730

731 **Fig. 1.** Management zones in a mature oil palm plantation. **(a)** Four management zones
732 varying in terms of fertilization and aboveground C inputs. **(b)** Sampling points (red dots) in
733 the 9-year old plantation. Frond piles and harvest paths are absent in the 2- and 4-year old
734 plantations but two additional points (empty red dots) were sampled to assess palm root lateral
735 extension

736

737 **Fig. 2.** Soil organic C stocks separated between oil palm-derived soil organic carbon (C3-
738 derived SOC) and savanna-derived SOC (C4-derived C) depending on management zones
739 and soil depths after 9 years of oil palm cultivation on savanna grasslands. Mean values \pm SE
740 are represented (n = 5 for FP and HP, n = 4 for IZ and WC). FP, frond pile; HP, harvest path;
741 IZ, interzone; WC, weeded circle. Letters indicate significant differences between
742 management zones in total SOC (upper-case) and oil palm-derived SOC (black lower-case)
743 and savanna-derived SOC (white lower-case). The red continuous line shows the original
744 SOC level (\pm SE) in savanna grasslands (n = 10). The difference between red line and the top
745 of the stacked bars show the C losses over 9 years of oil palm cultivation

746

747 **Fig. 3.** Oil palm fine root development and oil palm-derived soil organic carbon (SOC) stocks.
748 **(a)** Oil palm fine root development with plantation age in the top 10 cm under frond piles
749 (FP), weeded circles (WC), harvest paths (HP), and interzones (IZ). Mean values \pm SE are
750 represented (n = 5 for FP and HP, n = 4 for IZ and WC). Letters indicate significant differences
751 between management zones in the 9-year old plantation; **(b)** relationship between oil palm-
752 derived SOC (C3-SOC) and fine root biomass under weeded circles. Overall linear regression
753 is indicated by the dashed line. Negative C3-SOC values result from the natural variation

754 standard of reference sites around the mean 13C value when C3-SOC accumulation is very
755 low or absent. Negative data were not set to zero to avoid increasing artificially the mean of
756 the respective depth and age and thus decreasing the overall slope of the relationship. The two
757 large arrows show the opposite effects of the plantation time and soil depth on the amount of
758 new C (C3) stabilized in soil

759

760 **Fig. 4.** Net oil-palm derived SOC (C3) stabilized per amount of cumulated fine root biomass
761 in each management zone after 9 years. Different letters indicate significant differences
762 between harvest paths (HP), interzones (IZ), frond piles (FP), and weeded circles (WC). Mean
763 values \pm SE are represented (n = 5 for FP and HP, n = 4 for IZ and WC)

764

765 **Fig. 5.** Relative effects of management zones on soil microorganisms in the 9-year old
766 plantation: basal respiration, metabolic quotient, microbial biomass C, and C:N ratio of
767 microbial biomass. Microbial variables in interzones (IZ), frond piles (FP), and weeded
768 circles (WC) were normalized with their respective mean value in the harvest paths (HP), that
769 is, the zone receiving neither C inputs nor nutrient applications. Specific respiration (basal
770 respiration divided by C content) is not represented because the effect of management zone
771 was not significant. Error bars represent SE (n = 5 for FP and HP, n = 4 for IZ and WC).
772 Letters indicate significant differences between management zones for each parameter

773

774 **Fig. 6.** Pearson correlation matrix among soil variables in the top 10 cm. Correlation
775 performed on samples collected in the three management zones located at 4.5 m away from
776 palm trees (harvest paths, interzones, and frond piles). Variables are: basal respiration,
777 specific respiration, metabolic quotient, oil palm-derived (C3), and savanna-derived (C4)
778 SOC stocks, soil C and N contents (C, N), microbial biomass C and N (Cmic and Nmic), C:N

779 ratios of SOM (CN), K₂SO₄-extractable C (DOC), soil available P (P), and fine root biomass
780 stocks (Fine roots). Only significant correlations are represented ($p < .05$, $n = 14$)

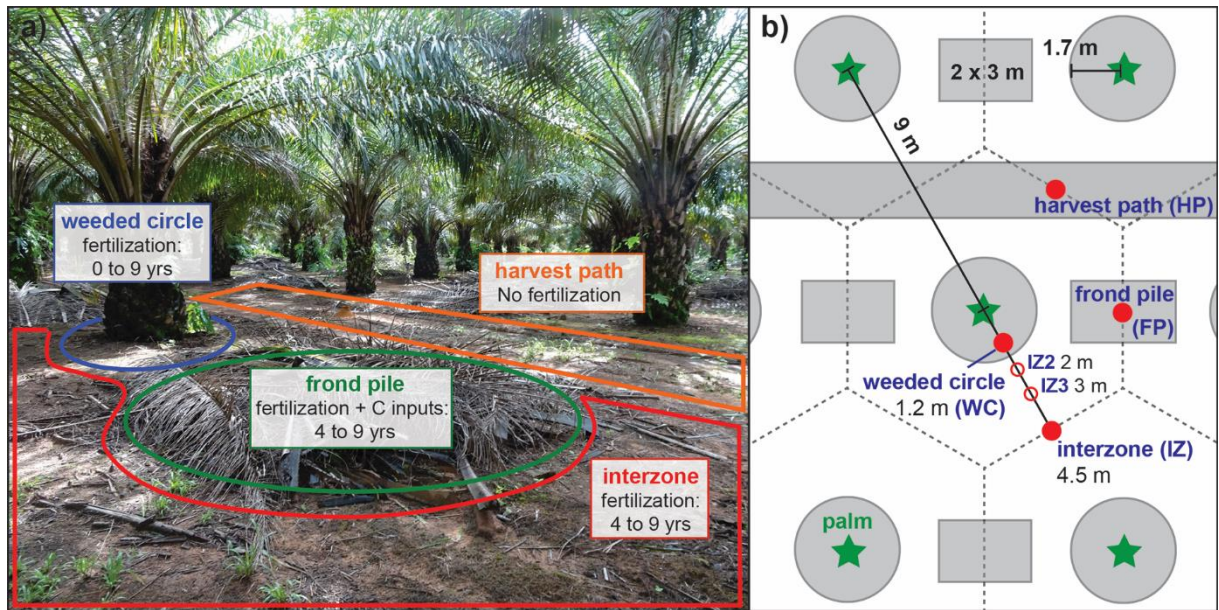
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782 **Fig. 7.** Drivers of oil palm-derived soil organic carbon (SOC) accumulation in the top 10 cm
783 of the three management zones located at 4.5 m away from palm trees (harvest paths,
784 interzones, and frond piles). Phosphorus availability was used as proxy for nutrient
785 availability. Fine roots correspond to fine root biomass stocks. Scores of samples on the first
786 axis (68%) of a principal component analysis (PCA) of all microbially related variables were
787 used as proxy for microbial effects. The C:N ratio of SOM was used as proxy for soil organic
788 matter quality. Solid arrows represent significant effects ($*p < .05$, $***p < .001$, $n = 14$) and
789 widths are proportional to the effect. Dashed arrows represent marginally effects ($p < .10$).
790 Non-significant relationships ($p > .10$) are not represented (nutrient availability to SOM
791 quality and SOM quality to soil microorganisms)

792

793 **Fig. 1.**

794

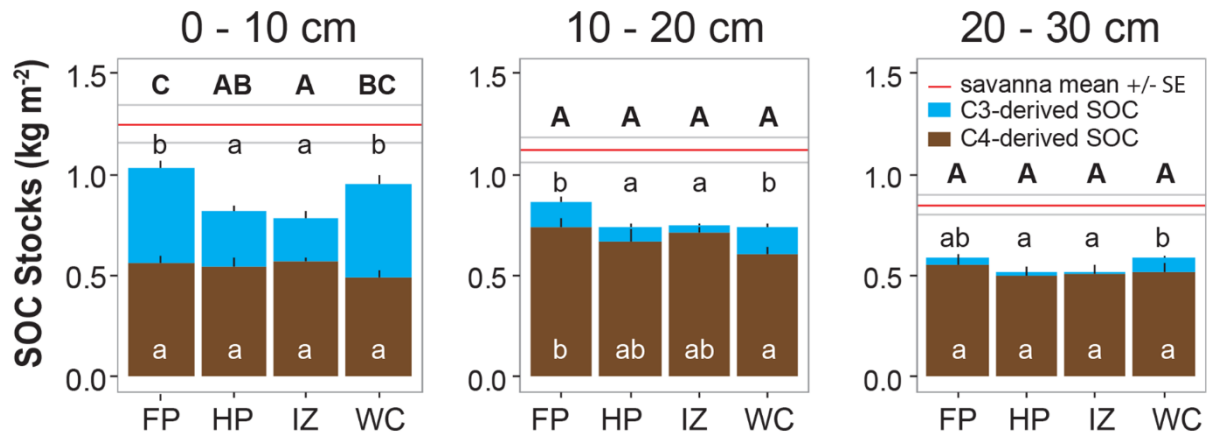


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797 **Fig. 2.**

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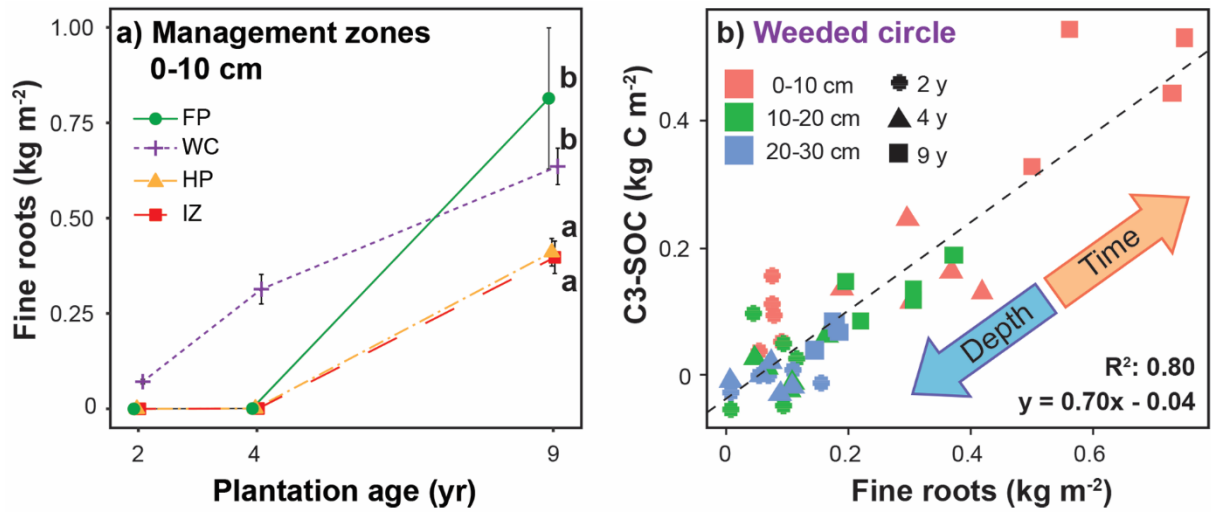


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801 **Fig. 3.**

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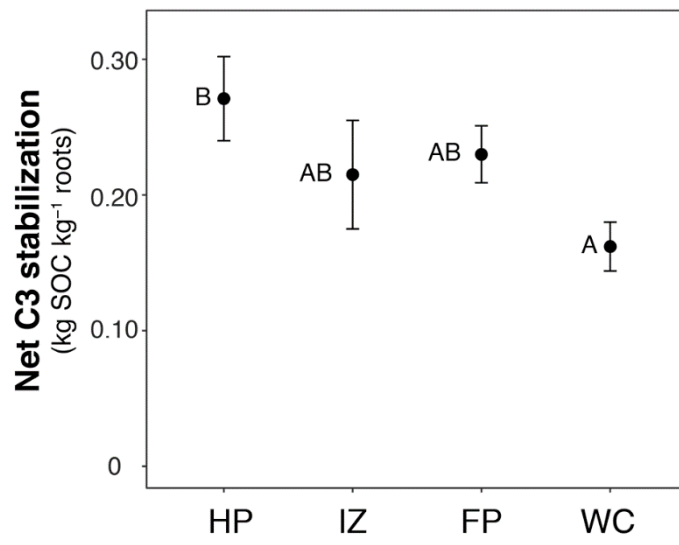


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805 **Fig. 4.**

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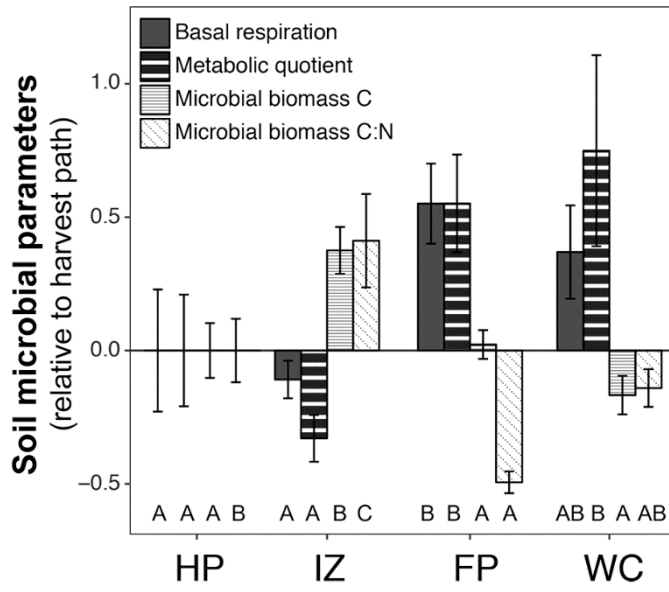


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809 **Fig. 5.**

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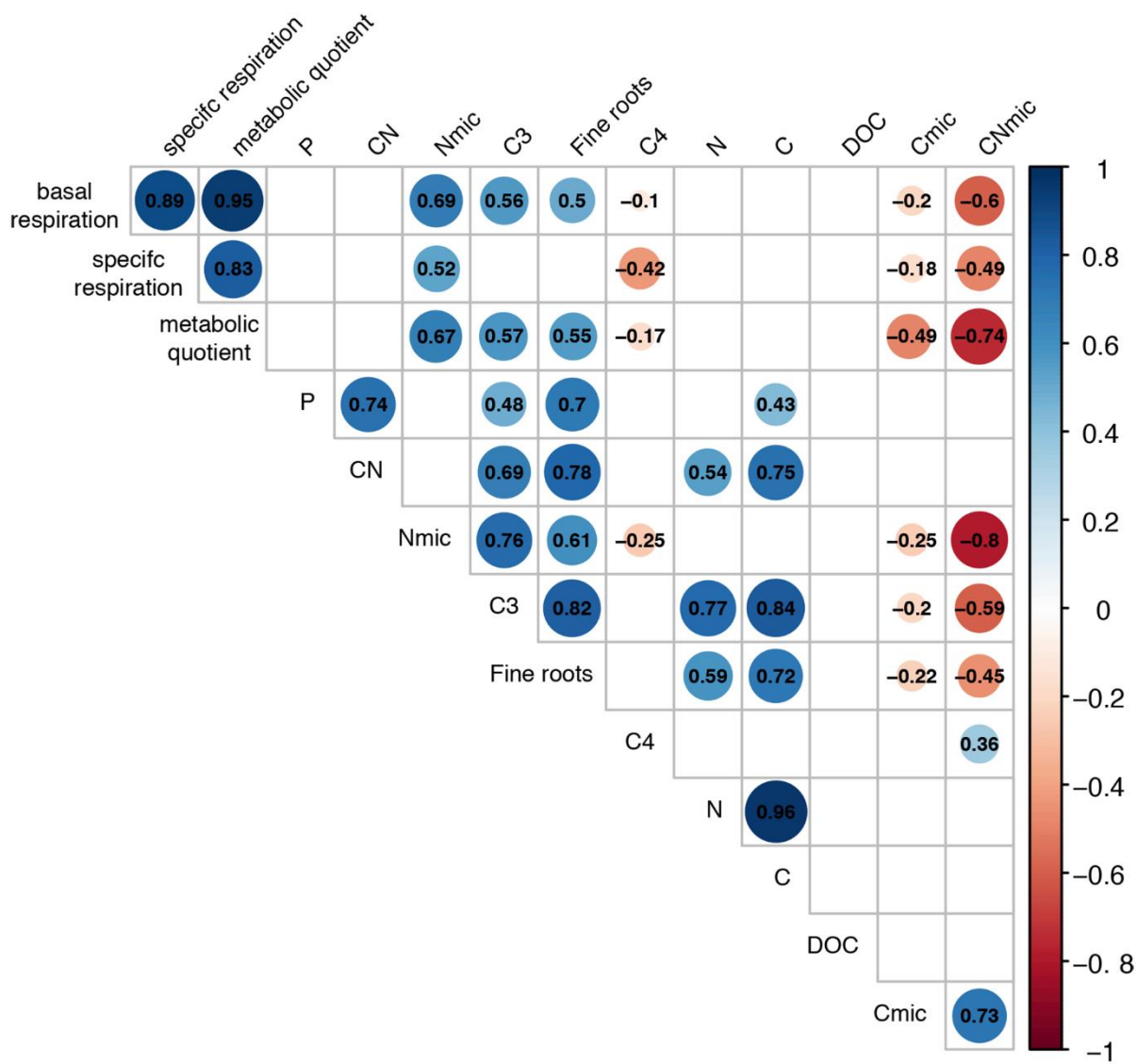


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813 **Fig. 6.**

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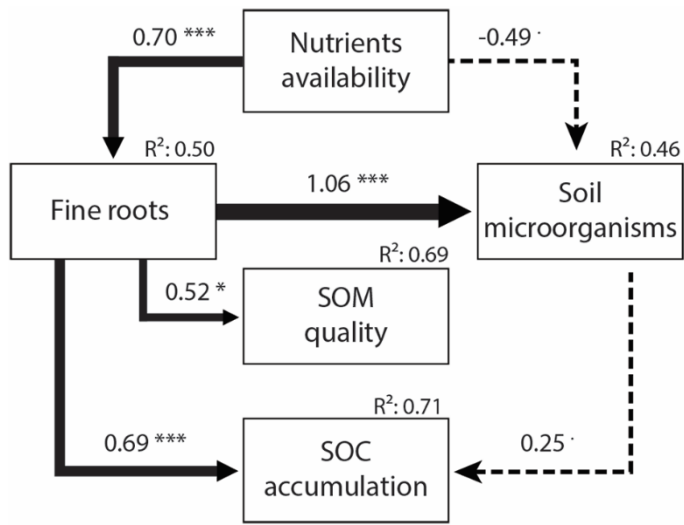


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816

817 **Fig. 7.**

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819

820