TITLE: Drivers of soil carbon stabilization in oil palm plantations

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ABSTRACT

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

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

1. INTRODUCTION

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

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

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

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

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

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

2. MATERIALS AND METHODS

2.1. Study area

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

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

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

2.2. Plantation management

Oil palm plantations had been established on native savannas whose soils were first loosened with a chisel plough (to a depth of 40 cm) and tilled with an overturning plough (10 cm). Liming and phosphate rocks were applied before planting palms. Oil palm trees had been 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 ($MgSO_4$), 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***

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

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

2.4. Soil analysis

198 Total C and nitrogen (N) contents in soil, as well as $\delta^{13}C$ 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 cm^3 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 NH_4F and 0.025 N HCl. Filtered extracts were mixed with a colorimetric
211 reagent ($(NH_4)_6Mo_7O_{24} - SnCl_2$) 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 $\delta^{13}C$ 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 $$f_{OP_d} = \frac{\delta^{13}C_{S_d} - \delta^{13}C_{NS_d}}{\delta^{13}C_{OP_b} - \delta^{13}C_{NS_b}}$$
220 where f_{OP_d} is the fraction of oil palm (C3)-derived SOC, $\delta^{13}C_{S_d}$ is the isotopic signature
221 measured in a soil sample at depth d, $\delta^{13}C_{NS_d}$ is the average isotopic signature at the

corresponding depth in natural savanna reference sites, $\delta^{13}C_{OP_b}$ is the averaged signature of oil palm fine roots in the mature oil palm plantation (mean = -28.2‰, standard deviation (SD) = 0.18, n = 9) and $\delta^{13}C_{NS_b}$ is the average isotopic signature of the aboveground and belowground savanna biomass determined on representative subsamples of aboveground biomass collected on 1 m^2 and fine roots collected with soil cores at each sampling point (mean = -13. 6 ‰, SD = 1.1, n = 19). This approach assumes that the ^{13}C fractionation occurring during the integration of biomass into SOC at each soil depth is the same for savanna and oil palm biomass (Pausch & Kuzyakov, 2012). No ^{13}C fractionation was observed between savanna plant biomass and savanna SOC in 0-10 cm layer (-13.7 ‰, SD = 0.5, n = 10).

2.6. Carbon stabilization per cumulative standing root biomass

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

2.7. Soil incubation

Microbial biomass was analysed after incubation of topsoils (0-10 cm) from the 9-year old plantation (zones FP, HP, IZ and WC). Twenty grams of dry soil were rewetted to 60% WHC and incubated at 25 °C for 31 days. Jars were ventilated and weighed every week and rewetted once to compensate for the evaporated water. Carbon and nitrogen (N) in microbial biomass were measured at the end of the incubation by the fumigation-extraction method (Vance et al., 1987). For C and N contents, 5 g of incubated soil were fumigated for 24 h with ethanol-free $CHCl_3$ in a desiccator. Soils were extracted by shaking 1 h in 25 ml solution of 0.5 M K_2SO_4 and then filtered. Non-fumigated samples were processed in parallel. Total extractable organic C and N were analysed with a TOC-N analyser (Shimadzu, Kyoto, Japan). Extractable C in the non-fumigated samples was assumed to represent dissolved organic carbon (DOC). Microbial biomass C and N were calculated as the difference between fumigated and non-fumigated samples, which were used also to calculate microbial C:N ratio. Microbial biomass C was corrected by dividing extractable C with a factor of 0.45 (Beck et al., 1997), N with a factor of 0.54 (Brookes, Landman, Pruden, & Jenkinson, 1985).

2.8. Basal respiration

Basal respiration of the rewetted samples was measured with the MicroResp™ kit (Campbell, Chapman, Cameron, Davidson, & Potts, 2003). Three analytical replicates of 0.5 g for each field replicate were taken from the incubation jars after rewetting and incubated in 96 deep-well plate in parallel to the incubation in jars. Soil was kept moist by a moist paper towel fixed on the plate. Respiration was measured 1, 2, 4, 8, 15, 18, 24 and 31 days after rewetting using a MicroResp™ kit (Campbell et al., 2003). To remove residual CO_2 in the wells, the plate was aerated with a fan before incubating for 6 h with the indicator plate on top (at 27 °C). The indicator plate was read before and after incubation with a spectrophotometer (Microplate reader BioTek SynergyMX) at 570 nm. Absorption calibration was done by

dissolving a known amount of $NaCO_3$ with 1 M HCl in excess in closed jars with eight microwells of the indicator plate for 6 h (Campbell et al., 2003).

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

$$Cmin = C_l(1 - e^{-tk_l}) + BR\ t$$

where *t* is the time, *Cmin* is the cumulative CO_2 mineralized to time t, C_l is the labile C pool released from sample preparation and re-wetting, k_l is the decomposition constant of the labile pool and *BR* is the basal respiration. The basal respiration of each field replicate was determined by fitting the model on the three analytical replicates. The metabolic quotient is the ratio of basal respiration over microbial biomass C (Cmic).

2.9. Statistical analyses

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

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

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

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

3. RESULTS

3.1. Soil organic carbon stocks and origin

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

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

3.2. Root development and C inputs

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

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

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

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

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

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

3.3. Soil microorganisms and fertility

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

Available P (Bray II) was an order of magnitude higher in weeded circles compared to the other zones, as expected by the higher fertilization application in that zone. Weeded circles also had the lowest amount of K_2SO_4-extractable C (DOC) despite high SOC content. (Table S1). Between the three zones (HP, IZ and FP) located at the same distance to the palm trees but varying in their management, P availability was two times lower in harvest paths (11.1 ± 0.3 µg g^{-1}) as compared to frond piles, but well above the P availability in native savanna sites (2.2 ± 0.3 µg g^{-1}), despite the absence of direct fertilization. The DOC amount was similar between the three zones and the C:N ratio was 1 unit higher under frond piles, indicating that only small change in SOC quality occurred between management zones.

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

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

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

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

4. DISCUSSION

4.1. Drivers of SOC stabilization

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

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

4.3. Increasing SOC stocks

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

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

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

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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TABLES

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

Weeded circles Depths *cm*	OP-derived SOC per year *g SOC m^{-2} yr^{-1}*	R^2	OP-derived SOC per fine roots *g SOC g^{-1} roots*	R^2	OP-derived SOC per cumulative fine roots *g SOC g^{-1} roots*	R^2
0-10 (n=14)	54 ± 6	0.85	0.62 ± 0.10	0.76	0.14 ± 0.02	0.86
10-20 (n=15)	18 ± 6	0.55	0.53 ± 0.11	0.60	0.11 ± 0.02	0.59
20-30 (n=15)	12 ± 2	0.75	0.50 ± 0.11	0.57	0.11 ± 0.01	0.80

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 ± 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 (±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 ± 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 ± 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 ($p < .05$, $n = 14$)
781
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

Fig. 1.

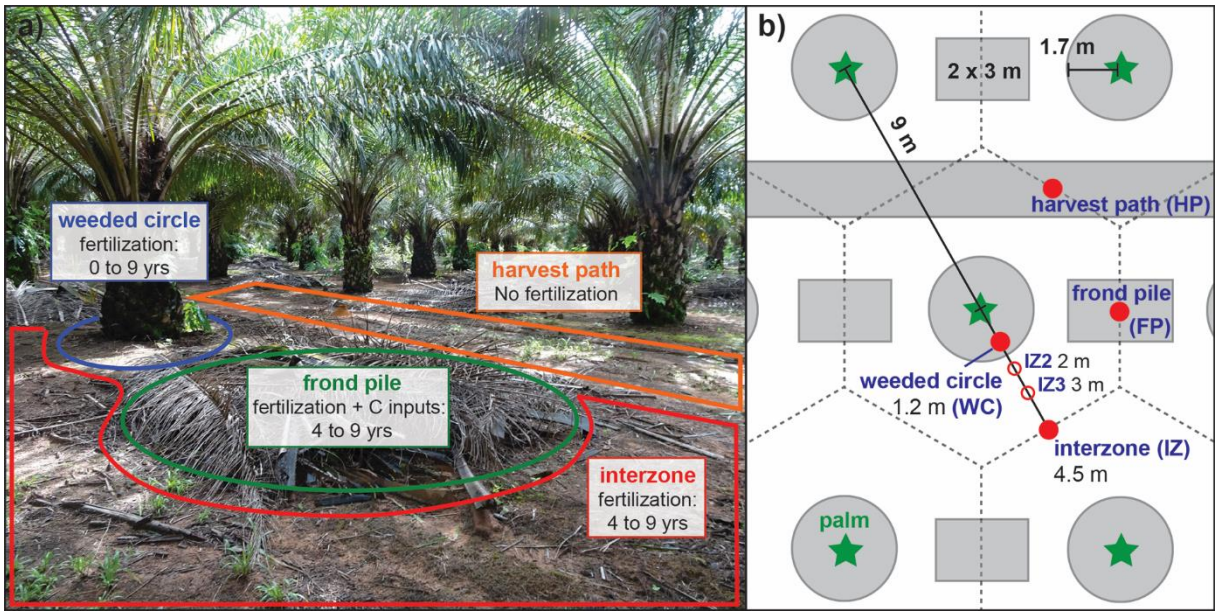
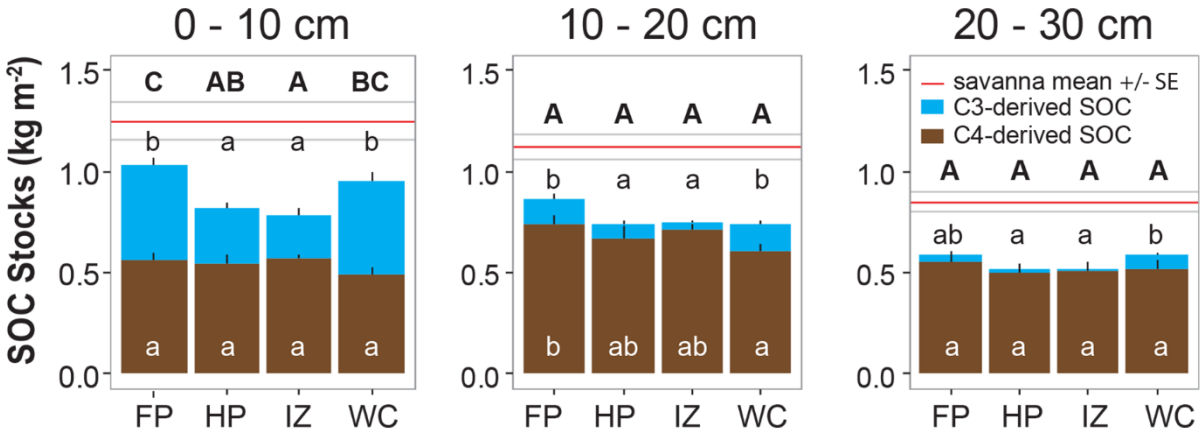
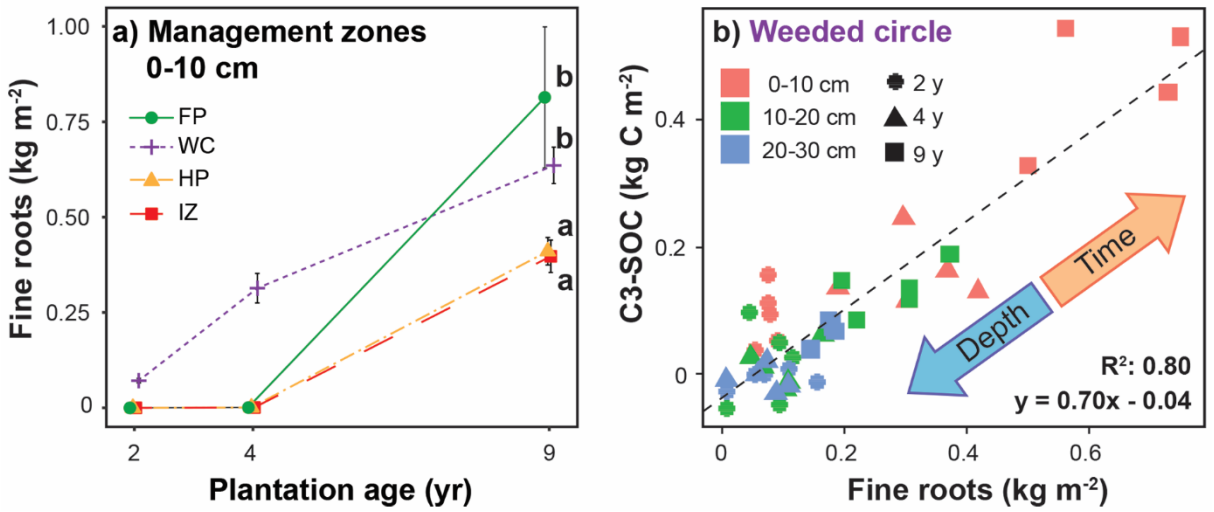

a)
weeded circle
fertilization:
0 to 9 yrs
harvest path
No fertilization
frond pile
fertilization + C inputs:
4 to 9 yrs
interzone
fertilization:
4 to 9 yrs
b)
2 x 3 m
1.7 m
9 m
harvest path (HP)
frond pile
(FP)
IZ2 2 m
IZ3 3 m
weeded circle
1.2 m (WC)
interzone (IZ)
4.5 m
palm

Fig. 2.


0 - 10 cm
10 - 20 cm
20 - 30 cm
SOC Stocks (kg m-2)
savanna mean +/- SE
C3-derived SOC
C4-derived SOC
FP
HP
IZ
WC

801 **Fig. 3.**

802

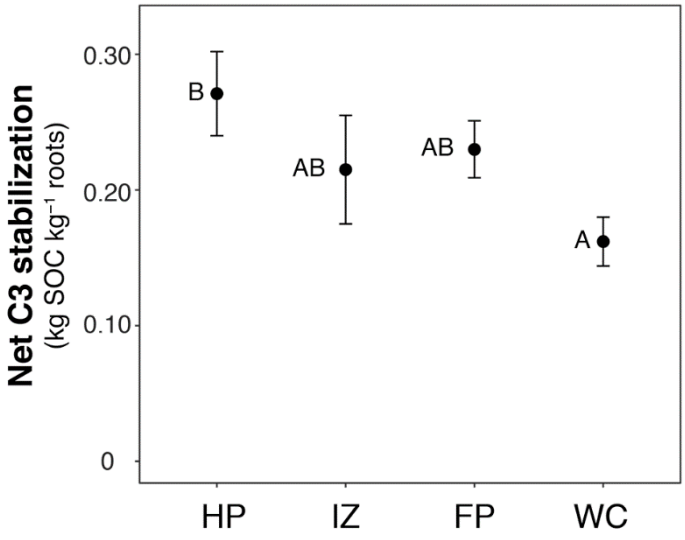


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805 **Fig. 4.**

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Fig. 5.

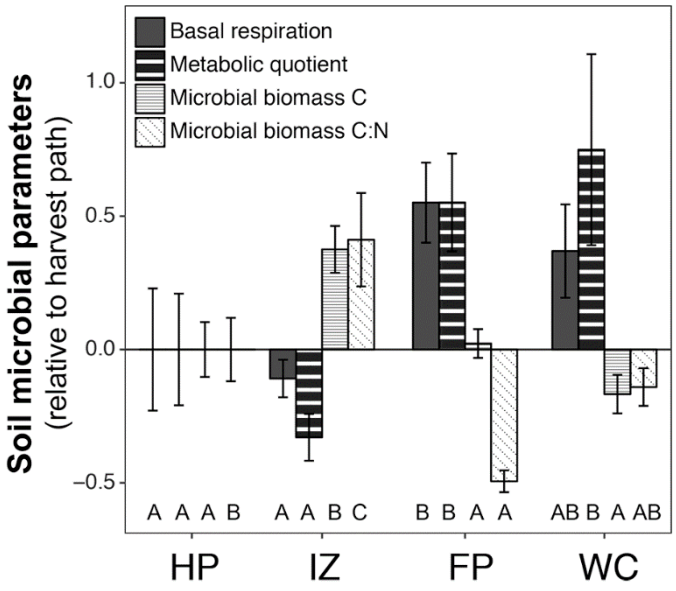
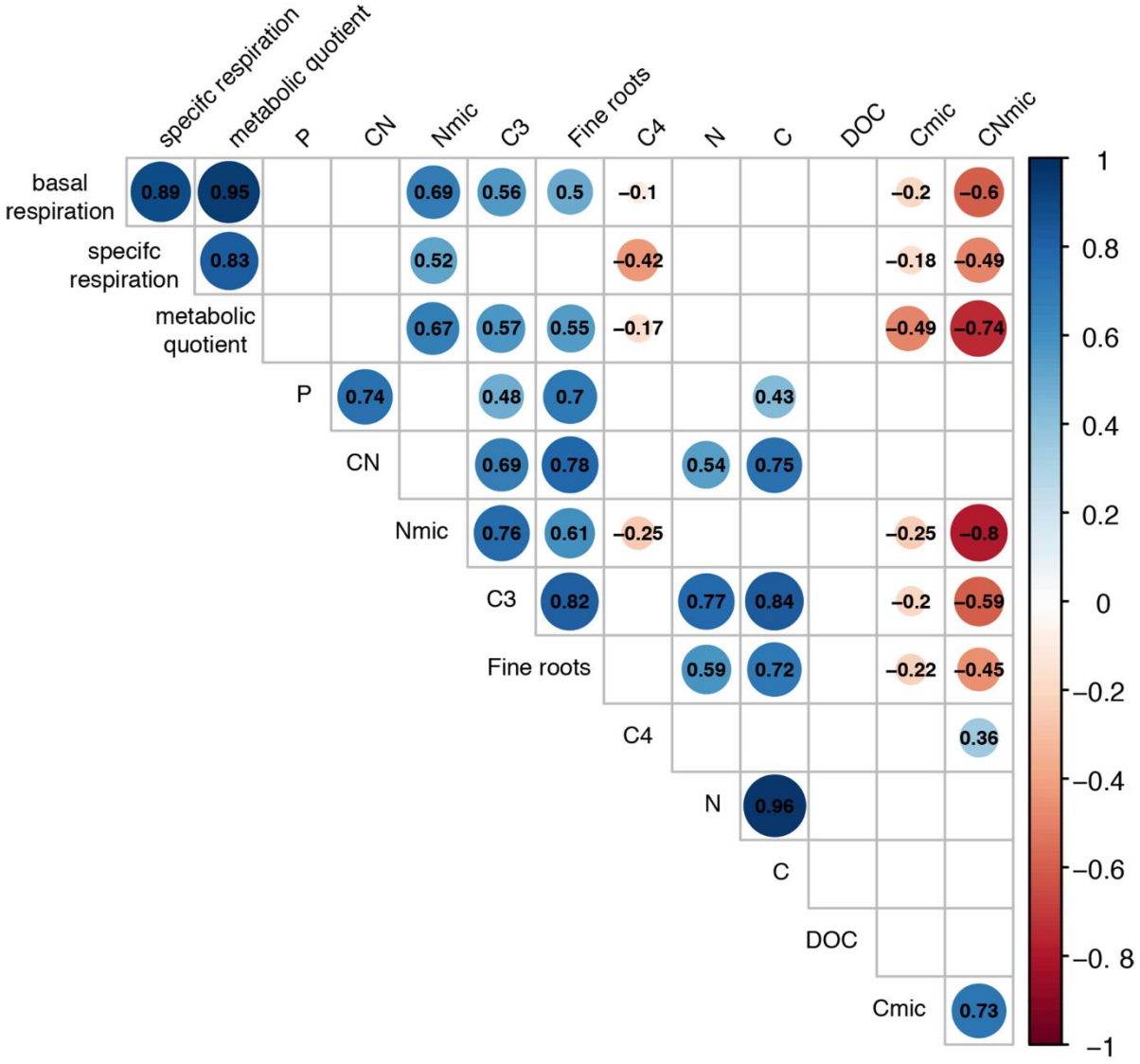
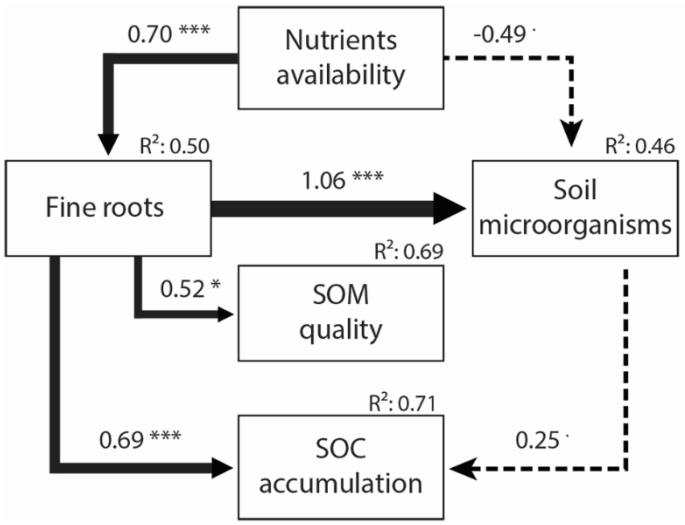

Basal respiration
Metabolic quotient
Microbial biomass C
Microbial biomass C:N
Soil microbial parameters
(relative to harvest path)
1.0
0.5
0.0
−0.5
A A A B
A A B C
B B A A
AB B A AB
HP
IZ
FP
WC

Fig. 6.


specifc respiration
metabolic quotient
P
CN
Nmic
C3
Fine roots
C4
N
C
DOC
Cmic
CNmic
basal respiration
0.89 0.95 0.69 0.56 0.5 −0.1 −0.2 −0.6
specifc respiration
0.83 0.52 −0.42 −0.18 −0.49
metabolic quotient
0.67 0.57 0.55 −0.17 −0.49 −0.74
P
0.74 0.48 0.7 0.43
CN
0.69 0.78 0.54 0.75
Nmic
0.76 0.61 −0.25 −0.25 −0.8
C3
0.82 0.77 0.84 −0.2 −0.59
Fine roots
0.59 0.72 −0.22 −0.45
C4
0.36
N
0.96
C
DOC
Cmic
0.73
1
0.8
0.6
0.4
0.2
0
−0.2
−0.4
−0.6
−0. 8
−1

817 **Fig. 7.**

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