



Root litter decomposition in a sub-Saharan agroforestry parkland dominated by *Faidherbia albida*

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ABSTRACT

In agroforestry systems, fine roots grow at several depths due to the mixture of trees and annual crops. The decomposition of fine roots contributes to soil organic carbon stocks and may impact soil fertility, particularly in poor soils, such as those encountered in sub-Saharan regions. The aim of our study was to measure the decomposition rate of root litter from annual and perennial species according to soil depth and location under and far from trees in a sub-Saharan agroforestry parkland.

Soil characteristics under and far from the trees were analysed from topsoil to 200 cm depth. *Faidherbia* tree, pearl millet and cowpea root litter samples were buried in litterbags for 15 months at 20, 40, 90 and 180 cm depths.

Root litter decomposition was mainly impacted by soil moisture and soil depth. *Faidherbia* decomposed more slowly ($36 \pm 12\%$ remaining mass after 15 months) than cowpea and pearl millet roots ($23 \pm 7\%$ and $29 \pm 11\%$ respectively). Pearl millet aboveground biomass, at harvesting time, was twice as high under (992 g m^{-2}) than far (433 g m^{-2}) from the tree, and belowground biomass (0–200 cm of depth) was 30.9 g m^{-2} and 19.6 g m^{-2} under and far from the tree, respectively. *Faidherbia* fine roots contributed slightly (p-value < 0.1) to higher stocks of C under the tree ($7761 \pm 346 \text{ g m}^{-2}$) than far from it ($5425 \pm 558 \text{ g m}^{-2}$) and from 0 cm down to 200 cm depth.

1. Introduction

In the current context of global warming, soil carbon (C) sequestration can contribute to mitigating the greenhouse effect (Nair et al. 2009a, 2009b; Chenu et al., 2019). In the tropics, C sequestration can more specifically contribute to the improvement of food security and to climate change adaptation (Paustian et al., 2016). Tropical soils are characterized by lower nutrient contents (Feller and Beare 1997) and more rapid C turnover than those in temperate systems (Six et al., 2002). A recent synthesis based on 48 studies performed on tropical soils from 13 countries demonstrated that the main determinants of soil organic carbon (SOC) accumulation were C inputs, duration of the experiments and management practices (Fujisaki et al., 2018). However, this synthesis did not consider agroforestry practices due to the lack of references, although agroforestry is assumed to enhance C storage in soils (Smith et al., 2014). Increasing soil C sequestration is a current

challenge in highly weathered tropical soils with low C contents, and agroforestry practices may contribute to overcoming this challenge.

In agroforestry systems, the diversity of the plant species and new ecological niches for biodiversity (Leaky 1996) lead to an enrichment of aerial, root and microbial biomasses (Nair et al., 2009b; Lagerlöf et al., 2014) with a trade-off between soil fertility improvement and competition for growth resources (Rao et al., 1997). C inputs in agroforestry systems are mostly related to the decomposition of aboveground biomass (tree litterfall and crop residues) and belowground biomass originating from tree and crop root turnover and/or mortality and rhizodeposition (Kuznyakov and Domanski 2000). Cardinael (2015) estimated that tree and crop fine roots each contribute 30% to organic matter input in agroforestry systems. Fine roots are generally more recalcitrant than aerial aboveground biomass to soil microbial decomposition (Rasse et al., 2005; Bertrand et al., 2006; Freschet et al., 2013), and they have the potential to increase soil C stocks. While several

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studies have demonstrated the chemical characteristics responsible for slow root decomposition rates (Machinet et al., 2009; Cotrufo et al., 2013; Prieto et al., 2016), the impact of soil depth has been less studied, although roots occur at different depths in the soil profile. This is particularly true for agroforestry systems where tree, herbaceous and crop roots colonize different soil layers, especially at depth (Cardinael et al., 2015; Germon et al., 2016; Battie-Laclau et al., 2020).

Root litter decomposition depends not only on litter quality but also on pedoclimatic conditions (Makkonen et al., 2012) and soil microbial communities and activity (Herman et al., 2012). These biotic and abiotic soil characteristics are strongly impacted by the introduction of trees in arable lands. The introduction of trees causes spatial heterogeneity in soil temperature and humidity (Monteith et al., 1991; Rao et al., 1997; Lin 2007) as well as soil microbial biomass abundance and composition (Chander et al., 1998; Guillot et al., 2021; Liu et al., 2019) and soil C stocks (Cardinael 2015). In a recent study performed in the same area as our study site, Roupsard et al. (2020) demonstrated that the whole pearl millet plant dry mass was 2.2 times higher under the *Faidherbia* tree crown than far from the tree. As a consequence, biomass inputs may be more important near trees, which could induce a modification of the soil chemical and physical properties. While the impact of trees on crop yield, climatic conditions and soil C stocks at a local scale was previously investigated in shallow soil horizons (Oelbermann et al., 2004; Oelbermann and Voroney 2007; Lin 2007; Roupsard et al., 2020), to our knowledge, no studies have investigated the impact of trees on deep soil characteristics or on tree and crop root decomposition.

Soil properties may vary with soil depth given that the total organic C content and microbial biomass decrease with depth (Hicks Pries et al., 2018). Soil temperature and moisture tend to be less subject to variations in deeper soil layers than in topsoil. Hicks Pries et al. (2018) showed that slower root decomposition could be responsible for higher stable C stocks at soil depth. A recent meta-analysis by Balesdent et al. (2018) performed on 112 grassland, forest and cropland sites demonstrated that the subsoil (30–100 cm depth) stored 47% of the C in the first metre of the soil profile. This deep C storage despite a lower litter input is related to root mortality and rhizodeposition and to the reduced decomposition rates at depth (Guenet et al., 2013). Data are lacking on root litter dynamics and C stocks in deep soil horizons, especially for tropical areas.

The aim of our study was thus to measure soil characteristics, including soil C stocks and the root decomposition rate, according to soil depth in a sub-Saharan agroforestry park dominated by *Faidherbia albida* trees and to account for the tree effect.

We hypothesized that (i) soil fertility, indicated by the C and nutrient contents, would be higher in the topsoil than in deeper soil layers and under trees than far from the trees due to the presence of leguminous tree species, (ii) the root litter decomposition rate would mainly depend on the plant species (i.e., root tissue quality), roots would decompose faster under trees and (iii) root litter would decompose more slowly in deep soil layers than in topsoil because of the stable pedoclimatic conditions.

2. Materials and methods

2.1. Study site

The “*Faidherbia*-Flux” collaborative observatory for greenhouse gas balance and ecosystem services (<https://ped.info/wikiObsSN/?Faidherbia-Flux>) is located in the natural agro-silvo-pastoral parkland of Sob (14°29'45N, 16°27'13W), 135 km East of Dakar, on the Bambey-Fatick transect, West Senegal, (Roupsard et al., 2020). The climate is sub-Saharan, with an average annual rainfall of 500 mm (Lalou et al., 2019) and an average temperature of 29.6 °C (Ndiaye et al., 2001). The soil temperature (°C) was measured with thermocouples buried at 0, 2, 5, 15, 30, 60, 100, 150 and 200 cm. The soil volumetric water content ($m^3_{H_2O} m^{-3}_{soil}$) was measured with TDR (time domain reflectometry)

moisture sensors buried at 15, 30, 50, 75, 100, 125, 150, 175 and 200 cm in an open area of the plot (far from the trees and close to the weather station). The rainfall was measured on site with an automatic tipping bucket (Texas Electronics, model TE525 mm). Data were recorded every 30 min over the entire study period. The average daily temperature and soil moisture and sum of rainfall were calculated (Fig. 1). The soil is a sandy tropical ferrallitic soil (Maignien 1965); it is classified as an Arenosol (IUSS Working group WRB, 2014). The water table is located at approximately 5–6 m depending on the season.

The studied agroforestry system was composed mainly of *Faidherbia albida* trees (85% occurrence), with a density of 6.8 trees ha⁻¹, which represents an average canopy cover of 5.14% measured over an area of 15 ha (Roupsard et al., 2020; Rahimi et al., 2021). *Faidherbia* trees were associated with groundnut (*Arachis hypogaea*) or pearl millet (*Pennisetum glaucum*) according to annual rotations. In June 2018, pearl millet was manually sown in the studied plot at a distance of 80 cm between each sowing pocket. Cowpea (*Vigna unguiculata*) was sown at the same time in a neighbouring plot with the same soil type and climatic conditions. There was no amendment applied to these plots, and harvesting was conducted in October 2018.

2.2. Above- and belowground biomass sampling

The biomass sampling campaign was conducted in October 2018, immediately before the pearl millet crop harvest. According to the large volume of soil to excavate and sieve (each pit was 8 m³), only 2 pits could be prepared, one under and one far from a tree. We sampled 3 walls in each pit, thereby assuming independence of the results. The pit under the tree was chosen under a *Faidherbia* individual representative of the tree population (Diatta 2021), with a height of 13.5 m and a circumference at breast height of 2.84 m.

The aboveground parts of pearl millet were collected in two subplots, each measuring 2 m × 2 m. One subplot was located under the selected *Faidherbia* tree crown (1.5 m from the trunk, crown radius of 5 m), whereas the second subplot was located far from any tree and at a minimum distance of 30 m from the first subplot. The subplots used for biomass quantification were at the same location as the pits. Each subplot included four pearl millet pockets. The vegetative biomass was split into ears, stems, leaves and stumps. All samples were oven-dried for 48 h at 65 °C before weighing.

After the aboveground biomass was sampled, two pits of 2 m × 2 m × 2 m were dug at the same locations. For each pit, roots were sorted by manually sieving the soil at 2 mm from a total soil volume of 8 m³ and split according to the plant species (pearl millet and *Faidherbia* tree) and the corresponding soil layer (0–40 cm, 40–100 cm, 100–150 cm and 150–200 cm). Given the small quantity of pearl millet roots found at great depth, the root biomasses of pearl millet in soil layers 100–150 and 150–200 cm were summed for each profile. Then, *Faidherbia* roots were sorted manually, and their diameter (D) was measured with a digital calliper to separate fine roots (D < 2 mm) from medium roots (10 mm > D ≥ 2 mm). All samples were washed on a 0.5 mm sieve and oven-dried for 48 h at 65 °C before weighing. The belowground biomass was assessed for 2 subplots × 2 plant species × 4 soil layers (× 2 root diameter categories for *Faidherbia*) after correction for the ash content. To this end, a subsample of 1 g of the washed root sample was burned at 500 °C for 4 h to remove organic matter, and the remaining mineral ash was weighed and deducted from the dry root mass.

Supplementary roots were collected between 0 and 40 cm depth in the neighbouring plot planted with cowpea and prepared as described above for millet and *Faidherbia* roots.

2.3. Litterbag experiment

We performed a 464-day root litter decomposition experiment with fine roots of *Faidherbia* tree, cowpea and pearl millet. A subsample of 1.5 g root litter was inserted in 10 cm × 20 cm nylon mesh screens of 1

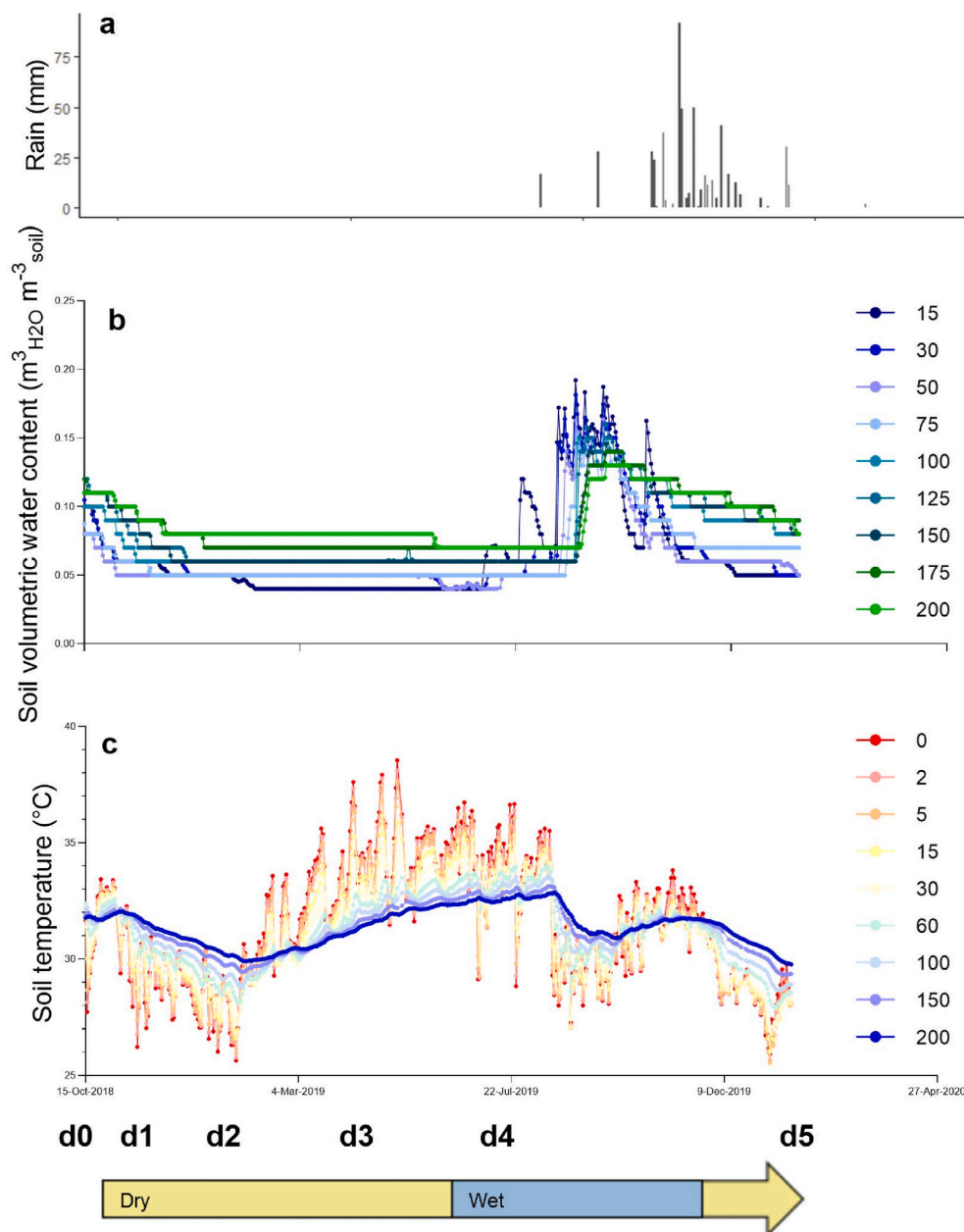


Fig. 1. Dynamics of rainfall (a), volumetric soil water content (b) and soil temperature (c) over time according to soil depth (from the topsoil to 200 cm deep) from the beginning (d0: 10/15/18) to the end of the experiment (d5: 01/22/20). On the x-axis, d0 to d5 correspond to the sampling dates after 1.5 (d1), 3 (d2), 6 (d3), 9 (d4) and 15 (d5) months of decomposition. Data are presented as daily averages. The wet season is represented in blue, and the dry season is represented in yellow. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

mm (Diatex), hereafter referred to as root litterbags. The mesh size of 1 mm allowed all decomposer communities, including small invertebrates, to penetrate the nylon mesh and establish themselves on the decomposing roots (Handa et al., 2014). On October 15th, 2018, corresponding to the harvest period, three litterbag replicates per plant species (Faidherbia tree, pearl millet or cowpea) were buried at four soil depths (20, 40, 90 and 180 cm) on 3 different walls (east, north and west walls) in each subplot (located under and far from the tree). The litterbags were buried at approximately 50 cm perpendicular to the pit walls to prevent desiccation or temperature fluctuations as much as possible. Each hole made to insert the litterbags perpendicular to the pit wall was filled with soil from the same hole. Each litterbag was replicated five times to allow five sampling campaigns (d1 to d5), which were scheduled after 1.5, 3, 6, 9 and 15 months of root decomposition. The first months of decomposition corresponded to the dry season (d1 to d3), while the wet season started immediately before the fourth litterbag sampling (see Fig. 1). The last sampling occurred during the next dry season (d5).

In total, 3 plant species \times 2 locations (subplots) \times 4 soil depths \times 3 pit walls \times 5 sampling dates = 360 litterbags were buried. However, due to a shortage in the initial sampling of root biomass encountered in the pits, cowpea and Faidherbia litter samples were not buried at 40 and 90 cm and thus were not collected on all dates (see Fig. 2).

After litterbag collection, the remaining root litter was carefully retrieved, and the soil adhering to the decomposed roots was carefully removed by shaking by hand before being oven-dried for 48 h at 65 °C. Ash corrections were made on a subsample to remove soil particle contamination as previously described. The relative humidity of the soil around the litterbags was measured from the oven-dried soil samples. The remaining dry mass in each litterbag was calculated as

$$RDM = \frac{M_f}{M_i} \times 100$$

where RDM is the remaining dry mass (%), M_i is the initial litter dry mass (g) and M_f is the final litter dry mass (g).

The remaining root dry mass according to a time axis for each species

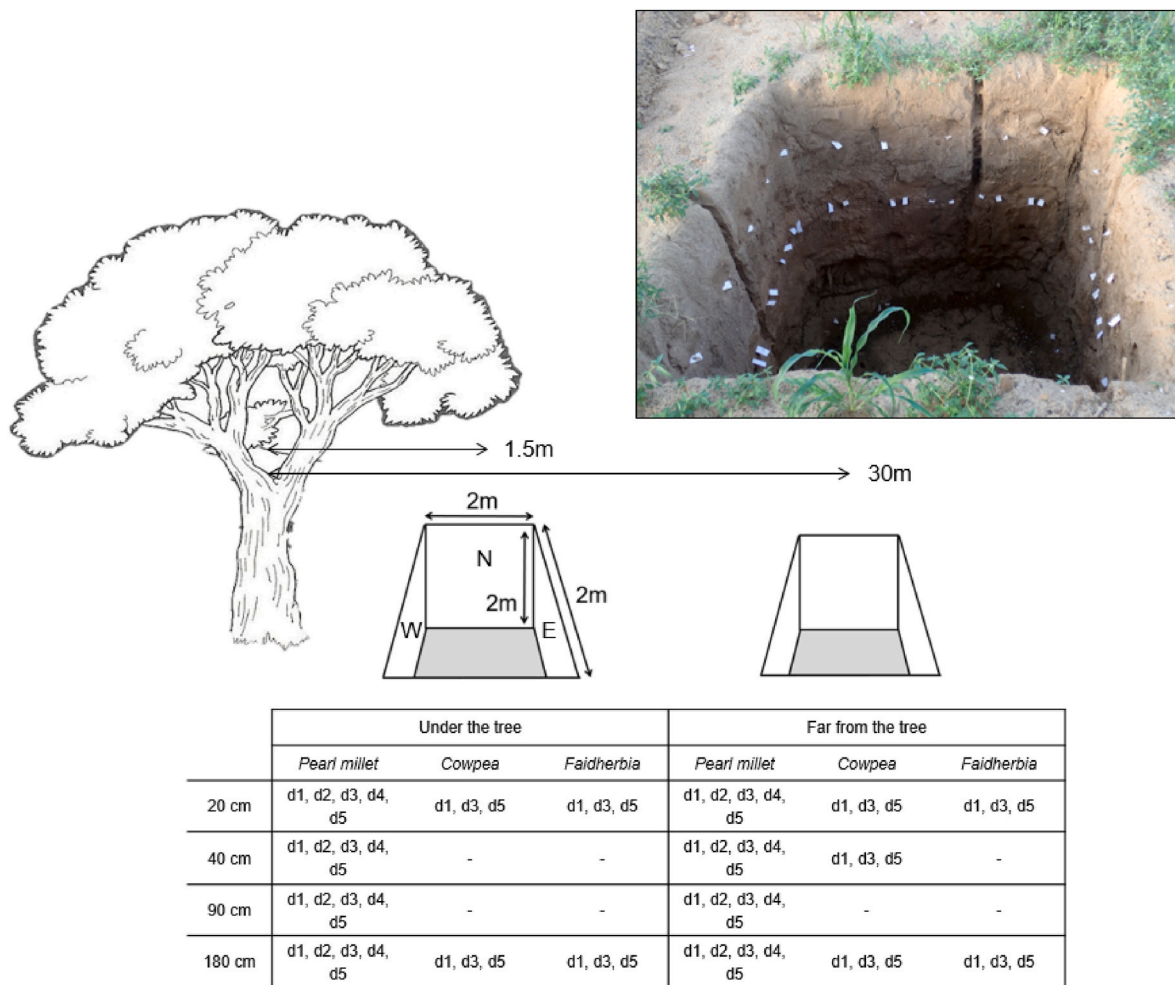


Fig. 2. Sampling strategy in the two pits (far from and under the tree), for each root litter type (pearl millet, cowpea and Faidherbia) at four depths (20, 40, 90 and 180 cm) and for five sampling dates (after 1.5 (d1), 3 (d2), 6 (d3), 9 (d4) and 15 (d5) months). Each litterbag was replicated on three pit walls (northern (N), eastern (E) and western (W) soil profiles). Missing treatments are due to root sample shortages.

at each location and each soil depth gave the decomposition kinetics, where the Y intercept was named d0. The time axis was expressed on standardized days depending on the soil temperature at each soil depth. The time was normalized by temperature using the method published by Mary et al. (1999) at a reference temperature of 25 °C, arbitrarily chosen as commonly used by Balesdent and Recous (1997):

$$D_{corr25} = \frac{D_{meas}}{e^{-K \times (T - T_{ref})}}$$

where D_{corr25} (days) is the time normalized at T_{ref} , T_{ref} (°C) is the reference temperature (25 °C), D_{meas} is the measured time (days), T (°C) is the average soil temperature of each day, and K is the thermal coefficient ($K = 0.115$ for kinetics of SOC decomposition at 25 °C (Balesdent and Recous 1997)). Then, for each root species at each location and each soil depth, the decomposition kinetics were determined by a regression between the remaining dry mass and standardized time. To better fit our data, two linear regressions were applied for individual decomposition kinetics: the first regression with a k_1 coefficient was based on the first sampling date (from d0 to d1), and the second regression had a k_2 coefficient (from d1 to d5). Two linear regressions \times 3 root species \times 2 locations \times 4 soil depths = 48 coefficients were obtained. Regressions with an R-squared value lower than 50% were removed from the dataset.

2.4. Initial litter quality

Initial root chemical qualities were determined for the three plant species (pearl millet, cowpea and Faidherbia tree). C fractions (soluble compounds, cellulose, hemicellulose and lignin) were assessed with a fibre analyser (Fibretherm®, Gerhardt) on a 500 mg root litter subsample following the Van Soest protocol (Goering and Van Soest 1970). Root C and N elemental composition was determined with an automatic elemental analyser (Flash, 2000, ThermoFisher Scientific) on 3 mg subsamples of root litter. For the total root P content, 50 mg of litter powder was mixed with 65% HNO₃ and mineralized for 15 min at 200 °C in a Milestone Ethos Easy microwave under standard and blank conditions. The total P content was quantified colorimetrically with the yellow vanadomolybdate assay (Koenig and Johnson 1942).

The proportion of C originating from roots and remaining in the soil after 15 months of decomposition was calculated for 2 species (pearl millet and Faidherbia fine roots) at both locations (under and far from the tree) and at 3 depths (0–40, 40–100 and 100–200 cm, which matched the root biomass sampling and litterbag experimental setup) by multiplying the root carbon content (%) and the remaining mass at d5 (%). Decomposition data were missing at 90 cm depth for Faidherbia, and an average proportion of C at 20 and 180 cm was thus used. Then, this calculated proportion was multiplied by the living root carbon stocks (gC m⁻³) to give the amount of remaining C originating from roots and remaining in the soil after 15 months of decomposition for

each species and at each depth. For pearl millet as an annual crop, the totality of the root carbon entered the soil at each harvest and thus at each year. For *Faidherbia* as a perennial tree, we considered that 0.56% of the root carbon was entering the soil each year according to the acacia root turnover (Jha and Prasad Mohapatra 2010). This calculation was not performed for cowpea because the root biomass in the soil profile was not assessed for pearl millet or for *Faidherbia*.

2.5. Soil sampling and analyses

The soil sampling campaign was conducted in late October 2018 immediately after the pits were dug. In each pit (under and far from the tree), in three out of four faces (taken as replicates), soil samples were collected at different depths (0–10 cm, 10–20 cm, 20–40 cm, 40–70 cm, 70–100 cm, 100–130 cm, 130–160 cm, 160–200 cm). The soil sampling was more detailed than the experimental design of the litterbags to obtain a precise characterization of the soil profile. Soil was sampled where the litterbags were buried. Each sample was analysed by the LAMA laboratory (IRD-US Imago, Dakar, Senegal) for total soil C and N contents by dry combustion (Matejovic 1997). The mineral C content was assumed to be insignificant, and the measured total soil C was thus associated with soil organic C. Soil pH was measured in a 1:2.5 soil-water suspension. Available phosphorus was determined according to the Olsen method and was measured by the malachite green method (Ohno and Zibilske 1991). Soil mineral N was extracted with a 1:4 soil⁻¹ M KCl solution, NO₃⁻ and NH₄⁺ were determined by continuous flow colorimetry (SKALARSA 3000 flow analyser), and the sum of NO₃⁻ and NH₄⁺ represented the mineral soil N content. Soil texture was determined based on five fractions (clay, silt (fine + coarse), sand (fine + coarse)).

The soil bulk density was assessed according to the cylinder method (Blake and Hartge 1986) in each pit (under and far from the tree) on two out of four faces (as replicates) at ten soil depths (10, 20, 40, 60, 80, 100, 120, 140, 160 and 180 cm).

SOC stocks were calculated at each location (under and far from the tree) and each soil depth following the 'M1' method described by Poellau et al. (2017) as follows:

$$C_{stock_ij} = BD_{mean} \times C_{tot} \times w$$

where C_{stock_ij} is the soil C stock at location j in soil layer i (g m⁻²), w is the width of soil layer i (m), BD_{mean} is the mean bulk density of soil layer i (g m⁻³) and C_{tot} is the amount of total soil C measured in soil layer i at location j (g g⁻¹soil). To compare the surface soil layers with the deep layers while the compaction was different due to ploughing of the topsoil layers, we also calculated the C stock at an equivalent soil mass following the method presented by Ellert and Bettany (1995).

The total SOC stock in the whole soil profile was calculated for each location as the sum of the SOC stock in each layer.

2.6. Statistical analyses

For each measurement, data are presented as the mean values ± standard deviation of 3 replicates. Whenever the location (far from and under the tree) had no significant effect according to the methods described below, the average value of 6 replicates was calculated instead. All statistical analyses were processed with R Software (version 4.0.2) (R Core Team 2020).

To analyse the effect of depth and location on soil characteristics, linear mixed models were applied to each soil variable, with soil depth and location as fixed factors and the 3 replicated profiles as random factors. Data from the same soil profile were considered dependent on each other. Post hoc Tukey tests allowed us to determine the significance of the differences between each category of soil depth and location. C stocks in both locations were compared for each soil layer with Wilcoxon rank sum tests, as required for comparisons between 2 populations with

3 individuals each.

The initial difference in the quality of the root litter from the three plant species was analysed with one-way analysis of variance for each variable (soluble fraction, hemicellulose, cellulose, lignin, total C, total N, and total P contents and C:N). To analyse the variations in the humidity of the soil in contact with the litterbags, a linear mixed model was applied to the relative humidity, with location, soil depth, plant root species and sampling date as fixed factors and the 3 replicated profiles as random factors. To analyse the effect of location, soil depth and plant species on root litter decomposition, linear mixed models were applied to the remaining litter dry mass on each sampling date and to the k1 and k2 decomposition rates, with soil depth, location and plant species as fixed factors and the 3 replicated profiles as random factors.

To analyse the carbon inputs from the roots (Fig. 10), linear mixed models were applied to the soil C stocks, to the tree living fine root C stocks, to the pearl millet living root C stocks and to the remaining C in the soil after 15 months of decomposition (all data in gC m⁻³), with location, soil depth and plant root species as fixed factors and the 3 replicated profiles as random factors. For all the linear mixed models and analyses of variance, *lme4* and *car* packages were used. The normality of the residues was always verified with a Shapiro-Wilk test, and the homogeneity of the variances was verified with a Bartlett test. When necessary (p-values < 5%), Box-Cox (*boxcox*) or Yeo Johnson (*jtrans*) transformations were applied.

A simple ordination of all the variables was conducted for a principal component analysis with the "vegan" and "factoextra" packages. Among the soil depths that were analysed for the initial soil characterization, only 4 depths were selected for this analysis (10–20, 20–40, 70–100 and 100–130 cm) to match the experimental design of the litterbags. Wilk's tests allowed the identification of qualitative variables (location, depth and plant species) that significantly separated the individuals with the "FactoInvestigate" package.

3. Results

3.1. Effects of depth and location on soil characteristics

The soil texture was globally very sandy, with more than 70% sand in every sample (Fig. 3), but the texture was significantly impacted by soil depth (Supplementary Table 1), with soils richer in clay and lower in coarse sand in the deeper layers (Fig. 3a). Location impacted only fine sand, with a higher content far from the tree (p-value = 1.94 × 10⁻²), while an interaction between soil depth and location was observed for the silt content (p-value = 7.63 × 10⁻⁵ combined with soil depth).

The total C and N contents were not significantly impacted by location (Supplementary Table 1). However, the soil total C and total N contents tended to be higher under the tree than far from the tree (Fig. 4a and b). In this poor Arenosol, the total soil C did not exceed 0.45% in the surface layer. At both locations, soil depth strongly affected the total C (F = 30.17, p-value = 3.0 × 10⁻¹¹) and N contents (F = 11.30, p-value = 1.2 × 10⁻⁶) with a strong decrease from a depth of 30 cm. The C:N ratio, soil pH, and soil available phosphorus and mineral N contents were impacted by the interaction of depth and location, while only the mineral N and C:N ratios were significantly affected by soil depth (Supplementary Table 1). In the first 20 cm, the C:N ratios increased from 12.7 to 14.0 far from the tree and then decreased to 8.7 at 180 cm, while under the tree, the C:N ratios increased from 11.0 at the surface to 14.3 at a depth of 1 m (Fig. 4c). Soil pH presented values ranging between 6 and 7 in the topsoil. Below 40 cm, soil under the tree presented higher pH values (6.9 ± 0.6 between 40 and 180 cm) than those far from the tree (5.7 ± 0.3) (Fig. 4d). As often occurs in tropical soils, available phosphorus was very low (less than 3 mg kg⁻¹) and significantly higher under than that far from the tree (F = 3.77, p-value = 5.6 × 10⁻³, Supplementary Table 1). The available phosphorus decreased with depth to less than 1 mg kg⁻¹ at 180 cm for both locations (Fig. 4f). Mineral N presented similar patterns, with average values of 5.5 ± 2.8

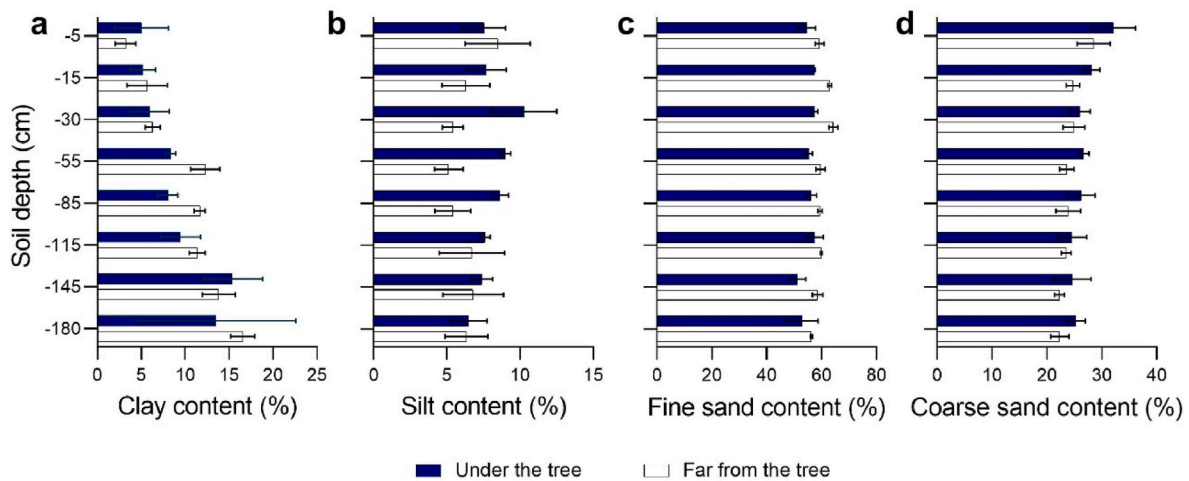


Fig. 3. Comparison of soil texture (%) variations in clay (a), silt (b), fine sand (c) and coarse sand (d) in the soil profile from topsoil to a depth of 180 cm in the pits under (dark) and far from the *Faidherbia* tree (white). Data are mean values from 3 pit walls, and error bars represent the standard deviation (n = 3).

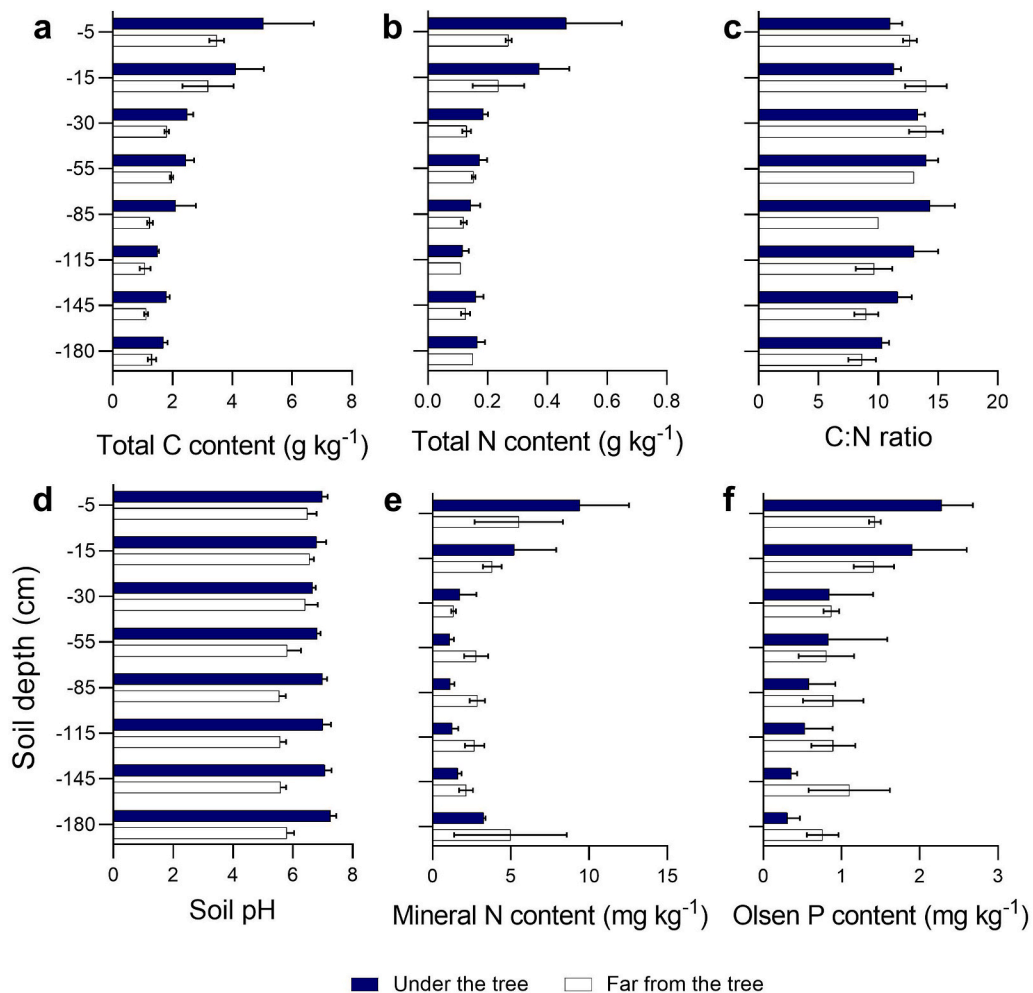


Fig. 4. Total C content (a), total N content (b), C:N ratio (c), soil pH (d), mineral N content (e) and available phosphorus content (f) in the soil profile from topsoil to a depth of 180 cm in the pits under (dark) and far from the tree (white). Data are mean values from 3 pit walls, and error bars represent the standard deviation (n = 3).

and $9.4 \pm 3.1 \text{ mg kg}^{-1}$ in the topsoil far from and under the tree and decreasing to 5.0 ± 3.6 and $3.3 \pm 0.1 \text{ mg kg}^{-1}$ at 180 cm, respectively (Fig. 4e).

Despite important differences in total C stocks within the whole profile under the tree ($7761 \pm 346 \text{ g m}^{-2}$, n = 3) compared to far from the tree ($5425 \pm 558 \text{ g m}^{-2}$, n = 3), the samples at each soil depth did not

Table 1

Total soil carbon stocks (g m^{-2}) of equivalent soil mass according to location (under or far from the tree) at different soil depths down to 200 cm. Data are mean values \pm standard deviation ($n = 3$). Significant differences between both locations for each soil layer were tested with Wilcoxon tests.

Soil depth	Carbon stocks on equivalent soil mass (g m^{-2})		Results of the tests of Wilcoxon	
	Under tree	Far from tree	W	p-value
0–10 cm	883 \pm 295	634 \pm 44	6	0.66
10–20 cm	712 \pm 164	543 \pm 145	8	0.2
20–40 cm	907 \pm 73	634 \pm 25	6	0.2
40–70 cm	1272 \pm 147	1064 \pm 30	9	0.1
70–100 cm	1083 \pm 353	684 \pm 52	9	0.1
100–130 cm	769 \pm 23	536 \pm 88	9	0.1
130–160 cm	920 \pm 57	623 \pm 34	9	0.1
160–200 cm	1214 \pm 101	919 \pm 97	9	0.1
Total stock	7761 \pm 346	5425 \pm 558	9	0.1

differ significantly between locations under and far from the tree (Table 1).

3.2. Above- and belowground biomass

Pearl millet biomass was higher under the tree than far from the tree (Fig. 5). The difference was mainly noteworthy for the aboveground parts, resulting in a lower R:S ratio (0.03 compared to 0.05 far from the tree). At both locations, millet roots were concentrated in the first 40 cm depth whereas under the tree, *Faidherbia* fine roots were concentrated

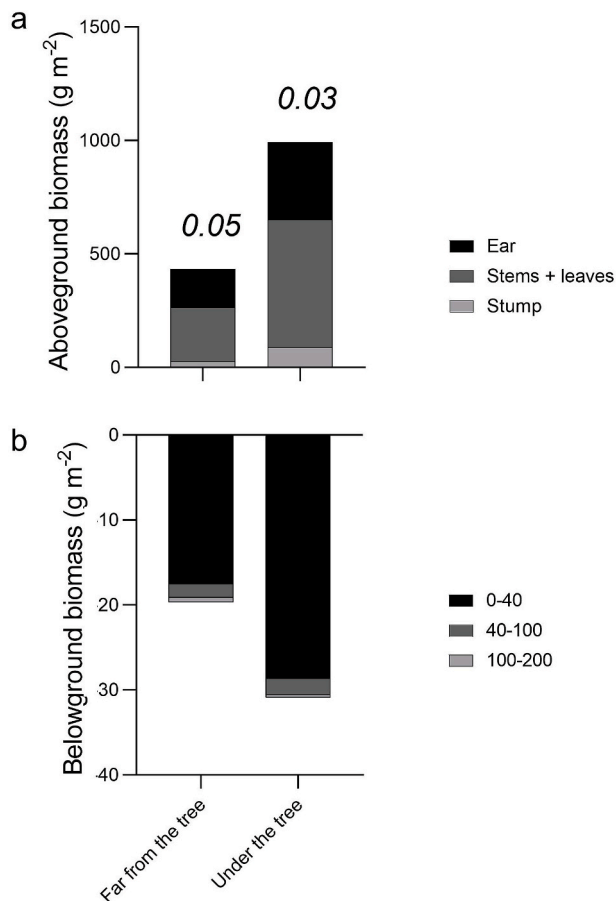


Fig. 5. Above- (a) and belowground (b) biomasses of pearl millet under (right) and far (left) from the *Faidherbia* tree according to organs (ears and grains, stems and leaves, stump) and soil depths (0–40, 40–100 and 100–200 cm). For each location, R:S ratios are indicated in italics.

below 40 cm depth. Far from the tree, tree roots were rare between 0 and 200 cm depth (Fig. 6).

3.3. Root litter quality, soil moisture and decomposition rates

Faidherbia litter was significantly enriched in lignin compared to cowpea and pearl millet litter (Table 2). Pearl millet roots presented a similar amount of lignin as in cowpea, while their soluble fraction was lower. However, the cellulose content was higher in pearl millet than in cowpea, while hemicellulose was not significantly different between the two crops. Large differences in the N content explained the important variations in C:N ratios, which varied from 13.0 for *Faidherbia* fine roots to 30.2 and 32.5 for cowpea and pearl millet roots, respectively.

The relative humidity of the soil in contact with the litterbags significantly increased with soil depth ($F = 337.9$, $p\text{-value} < 2.2 \times 10^{-16}$, Table 3), and it was higher under the tree than far from the tree ($F = 24.9$, $p\text{-value} = 7.3 \times 10^{-3}$, Table 3). The soil humidity was still high on d1 ($9.0 \pm 5.9 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{soil}$) from the previous wet season and decreased significantly from d1 to d3 ($F = 100.5$, $p\text{-value} = < 2.2 \times 10^{-16}$, Table 3). The wet season that started immediately before d4 increased the humidity of the soil in contact with the litterbags on d4 and d5.

Regarding root litter decomposition, no significant effect of location was observed on any date (Supplementary Table 2); thus, data were compiled for both locations.

After 15 months of the experiment, neither the crop nor the tree fine roots reached an asymptote; therefore, we described decomposition with 2 slopes k_1 and k_2 (linear fitting) rather than with one extinction coefficient (exponential fitting). After 1.5 months of fine root decomposition, i.e., d1, the root litterbags had lost almost half of their initial dry mass; then, with the dry season, the remaining fine root mass decreased more slowly from d1 to d5 and reached approximately 25% of the initial mass at the end of the experiment (Fig. 7). The remaining fine root mass on d2 (pearl millet only) was significantly impacted by depth ($F = 3.8$, $p\text{-value} = 4.8 \times 10^{-2}$), with a lower fine root remaining mass at a depth of 20 cm than at 40 cm and a lower fine root remaining mass at a depth of 90 cm than at 180 cm (Fig. 8a). On d5, the remaining mass was significantly higher for *Faidherbia* than for cowpea fine roots ($F = 3.9$, $p\text{-value} = 3.5 \times 10^{-2}$, Fig. 8b).

The k_1 coefficient of the first decomposition stage was significantly impacted by the plant species ($F = 3.9$, $p\text{-value} = 3.5 \times 10^{-2}$, data not shown), with higher coefficients for cowpea and lower coefficients for *Faidherbia*. The rate of fine root decomposition was also significantly impacted by soil depth in the case of pearl millet ($F = 7.4$, $p\text{-value} = 4.54 \times 10^{-3}$, Table 4), with lower values at 180 cm than at 20 cm depth. The cowpea fine root decomposition rate also decreased with soil depth but to a lesser extent than that of pearl millet ($F = 7.7$, $p\text{-value} = 2.13 \times 10^{-2}$, Table 4), while the fine root decomposition rate of the *Faidherbia* tree was only slightly impacted by depth (Table 4).

3.4. Relationships between fine root decomposition, soil characteristics and litter quality

The contribution of the main soil variables and the fine root decomposition rate to differences among soil depths is represented by the PCA (Fig. 9), which explained 50.5% of the dataset's variability. Individuals at each soil depth were well separated with no overlap between 95% confidence ellipses of three distinguished groups: 0–40 cm, 90 cm and 180 cm (Fig. 9, $p\text{-value} = 2.20 \times 10^{-9}$ for Wilk's test). The variables that best explained the separation between soil depths were C: N, sand, Olsen P and clay. The k_1 coefficient increased with these variables. These variables were not correlated (orthogonal) with k_2 , the soil pH or silt content (Fig. 9). Therefore, the first axis of the PCA best described variables that correlated with k_1 , and the second axis variables correlated with k_2 . Importantly, k_1 and k_2 were not correlated.

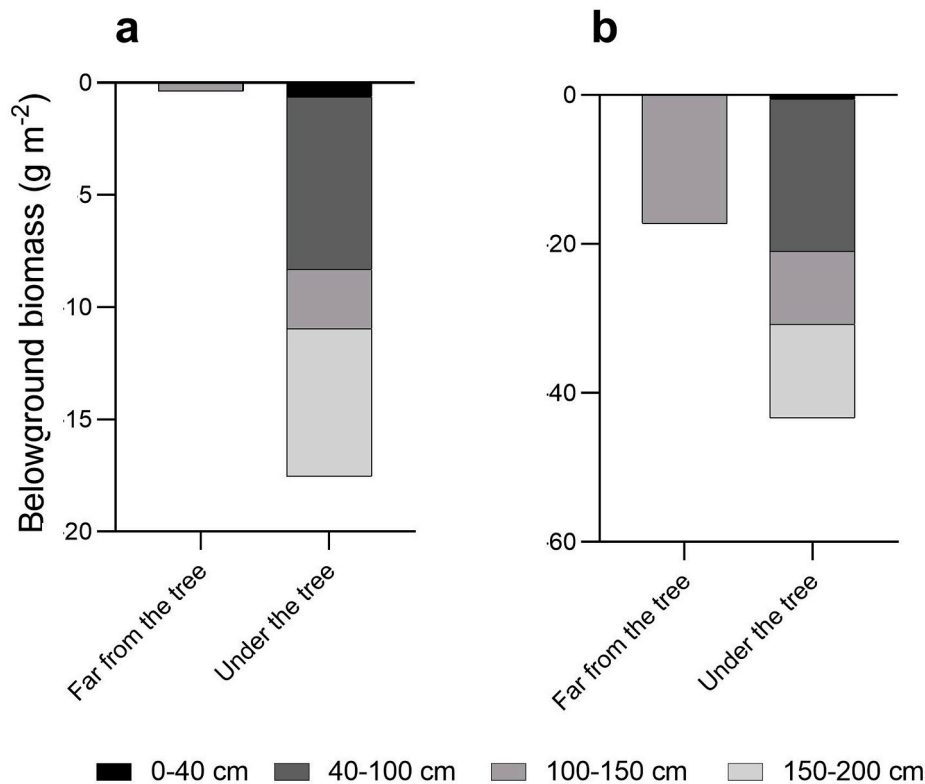


Fig. 6. Comparison of fine (a) and medium (b) root biomasses of *Faidherbia* under (right) and far (left) from the tree according to soil depth (0–40, 40–100, 100–150 and 150–200 cm).

Table 2

Initial values of biochemical qualities of the fine root litter added to the litterbags. Data are mean values \pm standard deviation ($n = 3$). Significant differences between root litter types were tested with one-way analyses of variance. ***, ** and * indicate the significance of the impact of the studied effects on litter quality with p -values < 0.001 , 0.01 , and 0.05 , respectively. Letters indicate differences between the 3 types of litter.

	Initial values			Statistics	
	Faidherbia	Pearl millet	Cowpea	F-value	p-value
Carbon fractions (% DM)					
Soluble fraction	14.5 \pm 2.7 ^a	13.9 \pm 2.2 ^a	27.1 \pm 2.2 ^b	29.3	8.1 \times 10 ⁻⁴ ***
Cellulose	19.4 \pm 2.4 ^a	37.9 \pm 2.4 ^b	21.3 \pm 4.4 ^a	29.9	7.6 \times 10 ⁻⁴ ***
Hemicellulose	14.2 \pm 1.9 ^a	27.4 \pm 2.2 ^{ab}	34.3 \pm 9.8 ^b	8.9	1.6 \times 10 ⁻² *
Lignine	51.9 \pm 4.1 ^b	20.8 \pm 2.1 ^a	17.3 \pm 4.4 ^a	82.6	4.3 \times 10 ⁻⁵ ***
Elemental composition (% DM)					
C	45.4 \pm 0.1 ^c	40.9 \pm 0.7 ^a	42.9 \pm 0.8 ^b	37.9	4.0 \times 10 ⁻⁴ ***
N	3.5 \pm 0.1 ^c	1.3 \pm 0.0 ^a	1.4 \pm 0.0 ^b	1779	4.8 \times 10 ⁻⁹ ***
P	0.09 \pm 0.0 ^{ab}	0.07 \pm 0.01 ^a	0.11 \pm 0.01 ^b	12.0	8.0 \times 10 ⁻³ **
C:N	13.0 \pm 0.3 ^a	32.5 \pm 0.9 ^c	30.2 \pm 0.3 ^b	981	2.8 \times 10 ⁻⁸ ***

4. Discussion

4.1. Impact of *Faidherbia albida* trees on soil characteristics

As expected for this type of soil, the total C and N contents were quite low (less than 0.5 and 0.05%, respectively), as previously described

(Barthès et al., 2006; Tounkara et al., 2020). The C and N contents decreased with soil depth and were higher under than far from the tree, as expected according to other agroforestry studies (Félix et al., 2018; Nair et al., 2009b), especially with *Faidherbia albida* (Dilla et al., 2019), but these differences were surprisingly not significant (considering p -value > 0.05). In the 0–40 cm soil layer, the soil C:N ratio was higher far from than that under the tree, whereas in the deeper layers, the opposite was true. These changes were associated with a large standard deviation, probably due to the low N concentration. Because *Faidherbia* leaf litter was shown to release high amounts of nutrients, especially N, during decomposition (Mubarak et al., 2008), the long-term effects of this litter may have contributed to a decrease in the surface soil C:N ratio, likely by increasing the bacterial pathway of decomposition (Rousk and Bååth 2007).

At a depth of 40–180 cm, the higher C:N ratio under the tree than far from it was also related to a lower soil mineral N content, while the yield of the pearl millet was almost 3 times higher under tree (Roupsard et al., 2020; Leroux et al., 2020). Due to higher pearl millet above- and belowground production, more mineral N could be taken up by the crop under the tree. However, with respect to pearl millet root distribution, the main difference between the locations under and far from the tree occurred in the topsoil (0–40 cm), and millet did not invest biomass at great depth under the tree, which is in agreement with the higher root: total biomass ratio far from the tree. Another possible explanation is that microorganisms may immobilize soil mineral N following an N-mining strategy (Chen et al., 2014) to mineralize soil organic matter or plant litter with a high C:N ratio. The total amounts of soil C and N were not influenced by tree presence, suggesting that the nature of the litter entering the soil instead of the soil organic matter (C and N) differed under and far from the tree and would be responsible for the hypothetical N-mining strategy. We did not separate roots or aboveground plant parts according to their location (under or far from the tree) before assessing their C and N contents. However, the fine and medium roots of

Table 3A

Differences in the volumetric humidity ($m^3_{H_2O} m^{-3}_{soil}$) of the soil in contact with the litterbags among soil depths (20, 40, 90 and 180 cm), plant species (pearl millet, *Faidherbia* tree, cowpea), locations (far from and under the tree) and sampling dates (d1 to d5). Data are mean values \pm standard deviation. The different lowercase letters indicate significant differences between the modalities, and ns indicates the absence of a significant effect.

	Soil volumetric humidity ($m^3_{H_2O} m^{-3}_{soil}$)					Statistics	
						F-value	P-value
Soil depth (cm)	20	40	90	180		337.9	$<2.2 \times 10^{-16}$
	0.020 ± 0.018^a	0.027 ± 0.024^b	0.045 ± 0.036^b	0.110 ± 0.051^c			
Root species	<i>Faidherbia</i>	Pearl millet	Cowpea		ns		
	0.060 ± 0.054	0.049 ± 0.046	0.051 ± 0.057				
Location	Far	Under				103.5	4.4×10^{-4}
	0.039 ± 0.036^a	0.069 ± 0.061^b					
Sampling date	d1	d2	d3	d4	d5	100.5	$<2.2 \times 10^{-16}$
	0.090 ± 0.059^d	0.058 ± 0.042^c	0.026 ± 0.028^a	0.042 ± 0.040^b	0.051 ± 0.053^{bc}		

Table 3B

Differences in the volumetric humidity ($m^3_{H_2O} m^{-3}_{soil}$) of the soil in contact with the litterbags between each location (far from and under the tree) on each sampling date (d1 to d5). Data are mean values \pm standard deviation. The different lowercase letters indicate significant differences between the modalities, and ns indicates the absence of a significant effect.

d1		d2		d3		d4		d5	
Far	Under	Far	Under	Far	Under	Far	Under	Far	Under
0.069 ± 0.039^a	0.113 ± 0.069^b	0.043 ± 0.029^a	0.070 ± 0.048^b	0.018 ± 0.021^a	0.035 ± 0.032^b	0.030 ± 0.019^a	0.051 ± 0.049^b	0.032 ± 0.033	0.072 ± 0.063
F = 16.9 p-value = 1.41×10^{-2}		F = 12.6 p-value = 2.22×10^{-2}		F = 15.2 p-value = 1.72×10^{-2}		F = 14.6 p-value = 1.68×10^{-2}		ns	

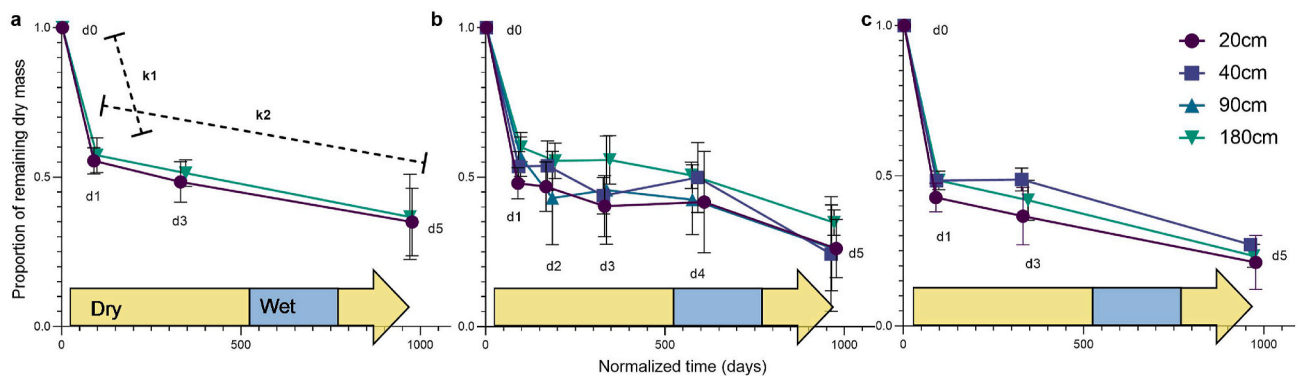


Fig. 7. Dynamics of root litter decomposition (after 1.5, 3, 6, 9 and 15 months) for the three plant species (*Faidherbia* tree (a), pearl millet (b) and cowpea (c)) at four soil depths (20, 40, 90, 180 cm). The wet season is represented in blue, and the dry season is represented in yellow. Data are mean values, and error bars are standard deviations ($n = 6$). Coefficients k_1 and k_2 are shown only on the left plot but were calculated for each regression. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Faidherbia were particularly abundant under the tree below a depth of 40 cm and had a low C:N ratio of 13. The low root C:N ratio can be explained by the high N availability in this N-fixing species, which would prevent a lack of N and thus hamper the N-mining strategy. However, the presence of N-binding materials such as lignin and polyphenols could restrict N accessibility and lead to a microbial N immobilization phase, as described during the leaf decomposition of a N-fixing tree by Teklay and Malmer (2004). Furthermore, the slow decomposition of *Faidherbia* roots due to the high lignin content could favour the development of K-strategy microorganisms dominated by fungi (Chen et al., 2014). However, without more information on the importance and nature of the soil microbial communities in comparison to total soil C, we cannot conclude the origin of the soil C:N changes.

Several soil fertility indicators, such as mineral N and Olsen P, were higher in the topsoil (0–40 cm) than at depth (40–200 cm) under the tree. The enrichment of nutrients in the topsoil under the *Faidherbia albida* tree was in agreement with the results found by Yengwe et al. (2018) and explained the higher crop yield under this tree. No remaining detritus of *Faidherbia* leaves was observed on the soil surface during the sampling period. This was due to the active livestock in this

silvo-agro-pastoral system removing the leaves, twigs and fruits from the ground during the litterfall season (April to July) due to the reverse phenology of this tree (Roupsard et al., 1999). However, ruminants tend to stand under trees, where excrement is deposited, which enriches the topsoil nutrient content under trees. At a depth of 50 cm, the lack of nutrients under trees compared to that far from trees could come from the increase in *Faidherbia* root biomass at the same depth and thus the increase in nutrient uptake at depth compared to the topsoil.

A significant interaction between the soil depth and location impacted the soil pH. Indeed, the higher soil pH under the tree compared with that far from the tree occurred mostly below a depth of 40 cm, while no significant differences were observed in the topsoil, as previously reported by Félix et al. (2018) for *Piliostigma* shrubs in Burkina Faso. In the 40–90 cm horizon, soil pH tended to increase under the tree (from 6.7 to 7.3), as found by Rao et al. (1997), while acidification (from 6.5 to 5.7) was recorded far from the tree. Sandy soils are poorly buffered (Wezel et al., 2000), and pH is sensitive to small variations in acid-basic reactions. Although our study did not allow us to conclude the mechanisms to explain the increase in pH under the tree, acidification of the soil profile far from the tree is an indicator of fertility degradation.

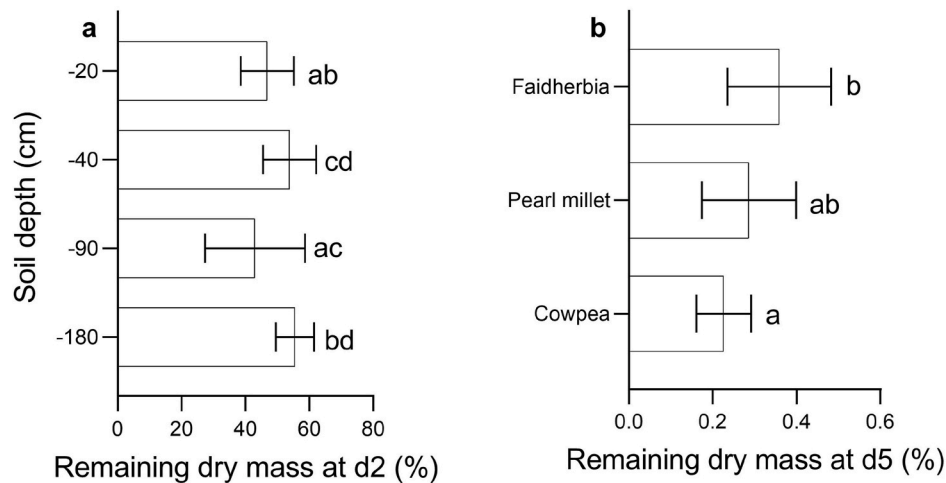


Fig. 8. Final root litter remaining mass (a) on d2 (01/17/2019) for pearl millet at four soil depths (20, 40, 90 and 180 cm) and (b) on d5 (01/22/2020) for three plant species (Faidherbia tree, pearl millet and cowpea) at all soil depths. Data are mean values, and error bars are standard deviations ($n = 3$). The different letters indicate significant differences in remaining dry mass for each soil depth (a) or for each plant species (b).

Table 4

The k_1 coefficient for each plant species (Faidherbia tree, pearl millet and cowpea) according to soil depth (20, 40, 90, 180 cm). Data are mean values ($n = 6$). The different lowercase letters indicate significant differences between the soil depths accompanied by their p -values for each plant species, and ns indicates the absence of a significant effect of soil depth.

	Soil depths (cm)				Statistics	
	20	40	90	180	F-value	P-value
Faidherbia	5.08×10^{-3}	–	–	4.44×10^{-3}	ns	
Pearl millet	5.93×10^{-3} b	5.17×10^{-3} a	4.55×10^{-3} a	4.16×10^{-3} a	7.4	4.54×10^{-3}
Cowpea	6.53×10^{-3} b	5.75×10^{-3} a	–	5.37×10^{-3} a	7.7	2.13×10^{-2}

Acidic soils are indeed known for their relatively low microbial abundance and diversity and low cation exchange capacity (Robson 2012) and could affect millet productivity.

4.2. Impact of soil depth on root litter decomposition

Due to the climatic conditions in the study area, root decomposition occurred rapidly after crop harvest (end of October 2018), while the soil was still moist from the previous wet season, and lasted for two months thereafter (January 2019). Then, the soil dried progressively from $9.0 \pm 5.9 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{soil}$ on d1 to $2.6 \pm 2.8 \text{ m}^3 \text{H}_2\text{O m}^{-3} \text{soil}$ on d3, as no rain occurred until the next wet season, which started in July 2019. Faster decomposition in wetter soils confirmed a previous report by Duthoit et al. (2020) regarding soil respiration. This moisture regime leads to two contrasting kinetics of decomposition, with a relatively rapid first phase (k_1) and a slower second phase (k_2), following the same time scale, similar to the few other studies conducted under similar environmental conditions (Mubarak et al. 2008, 2012). This result suggested that the labile part of the root litter decomposed quickly during the first phase of decomposition (k_1) when the soil was very wet. Then, the decomposition slowed (k_2) as the soil dried.

Soil moisture is a key factor controlling root decomposition and seems to be the main driver of decomposition kinetics after litter species, i.e., quality (Arrouays et al., 2002; Butenschoen et al., 2011). Because the humidity of the root litterbags was significantly higher for the individuals located under the tree due to tree shading, which reduced soil evaporation (Hasselquist et al., 2018), greater soil water infiltration

(Faye et al., 2020), the reduction of water runoff under the tree crown (Lal 1989) and the potential benefit of hydraulic redistribution through the Faidherbia root system (Bayala and Prieto 2020), we expected a slower fine root decomposition rate far from the tree than under the tree. This was not confirmed here. However, the lack of tree replicates may bias our results, and the study would need to be extended to a wider area of the park, including different tree sizes representing the local diversity of the parkland.

Root litter quality was the main factor controlling the rate of decomposition. *Faidherbia albida* roots decomposed more slowly than cowpea roots due to less soluble compounds and high lignin contents, as reported in Mubarak et al. (2012), while the root N content (higher in Faidherbia fine roots) did not seem to influence k_1 . Over a short period of time, soluble C drives the decomposition of plant residues (Bertrand et al. 2006, 2009; Moorhead et al., 2016; Liang et al., 2018), while the litter N content (C:N ratio) has no impact unless N limits decomposition (Recous et al., 1995; Bertrand et al., 2006), which does not seem to be the case here.

The remaining C after 15 months of decomposition accounted for root C inputs (Fig. 10) for 2 plant species (Faidherbia fine roots and pearl millet), at both locations (under and far from the tree) and at 3 soil layers (0–40, 40–100 and 100–200 cm of depth). The effect of all combined factors was significant ($F = 10.3$, p -value = 5.4×10^{-3} , Supplementary Table 2). Under the tree, Faidherbia root biomass was higher than far from the tree, and low decomposition rates of this perennial root litter were observed in the litterbags. Both of these factors resulted in higher C inputs from Faidherbia root litter under (0.62 gC m^{-2} between 0 and 200 cm of depth, Fig. 10) than far from the tree (0.02 gC m^{-2}), which could explain the tendency of higher soil C stocks under than far from the tree (Fig. 10, Table 1). Furthermore, the root C input was higher at depth than at the surface; between 100 and 200 cm depths, the amount of remaining C after 15 months of decomposition originating from Faidherbia root litter under the tree was 7 times higher than that at 20 cm. No significant C inputs from the Faidherbia root litter were noteworthy far from the tree. Due to a different root distribution, pearl millet presented the opposite trend. Pearl millet root C inputs were significantly higher at the soil surface than at depth, with no difference between the 2 locations (Fig. 10). The pearl millet crop provided 2.34 to 2.44 gC m^{-3} at 0–40 cm of depth through its roots. This amount is very low compared to the soil C stocks at the same depth (4708 gC m^{-3} far from the tree and 6429 gC m^{-3} under the tree), but it is repeated every growing season. The role in the soil carbon stocks of pearl millet in topsoil and of Faidherbia fine roots at depth was in agreement with that described by Jackson et al. (2017), attesting that fine roots contribute

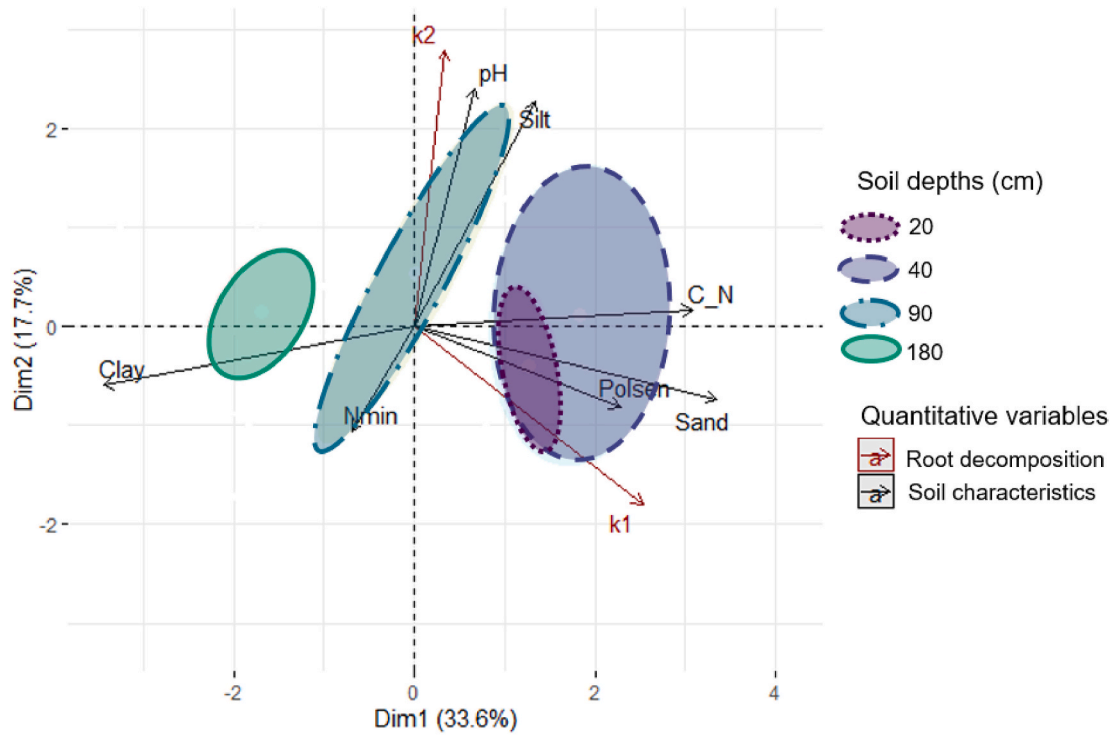


Fig. 9. Relationships between soil characteristics (clay, silt, sand, available P (as P_{olsen}) and mineral N (as N_{min}) contents, pH and the C:N ratio) and root decomposition (k_1 and k_2), according to the soil depth (20, 40, 90, 180 cm).

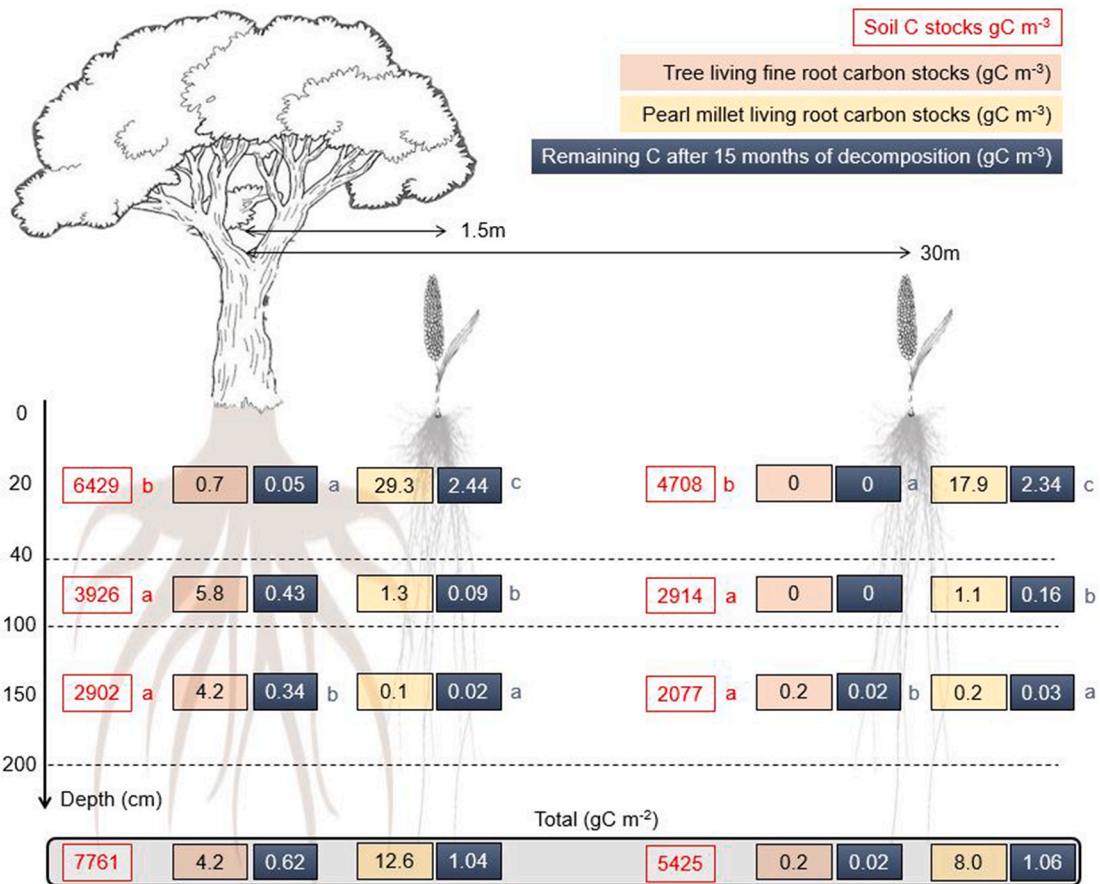


Fig. 10. Potential root C contribution to soil C stocks in one cultural season for *Faidherbia* and pearl millet according to the soil depth and at two locations: under (left) and far (right) from the tree. For each location, the different letters indicate significant differences in soil C stocks and in remaining C between the soil depths.

substantially to soil organic carbon storage. Future studies should prospect deeper soil depths to take into account a more representative cross-section of the tree root system. We hypothesized that soil depth would slow the fine root decomposition rate due to reduced microbial activity and moisture and temperature buffering, which was confirmed for the first phase of decomposition (k_1 was higher at 20 cm than at soil depths of 40, 90 and 180 cm for the three species). We did not measure microbial biomass C; however, several studies have reported its close relationships with the organic C content in soils (Insam and Domsch 1988; Webster et al., 2001; Ng et al., 2014). In the topsoil, more abundant microbial biomass and activity as well as drying/rewetting cycles that create a flush of C and microbial activity may explain the quicker decomposition rates (Miller et al., 2005; Sun et al., 2013). According to the PCA, the soil characteristics that best explained k_1 were sand, the Olsen P content and the soil C:N ratio, suggesting that the very low amount of P may have decreased the microbial activity at depth.

5. Conclusion

Root litter decomposition varied mostly according to soil depth, with litter quality and soil moisture being the main factors related to the decomposition coefficient k_1 in the first 1.5 months. Organic C originating from roots would be stored for a longer time period at depth than in the topsoil. Furthermore, tree root litter tended to be more recalcitrant than annual crop root litter and was more abundant below 40 cm, while annual roots were concentrated in the topsoil. Therefore, slow tree root decomposition at depth could play a role in increasing belowground C inputs and sequestration. In contrast, pearl millet induced root C inputs mainly in the topsoil and it did not depend on the location. The root decomposition rate was not affected by the location, but the tree fine root biomass and pearl millet vegetative production were higher under the tree than far from the tree. This difference resulted in higher soil carbon stocks under the tree than far from it.

In agroforestry systems, the diversity of plant species induces a great diversity of root qualities and thus various decomposition kinetics. Introducing trees in arable lands would globally increase root litter inputs while slowing root decomposition, especially at depth, and would thus increase the soil carbon storage potential of the system. Further research should focus on this aspect with replicated trees and different distances from the trees according to a gradient to confirm the influence of tree presence on root decomposition kinetics.

Credit authorship contribution statement

Siegwart Lorène: Data curation, Formal analysis, Writing – original draft. **Bertrand Isabelle:** Conceptualization, Validation, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Roupsard Olivier:** Writing – review & editing. **Duthoit Maxime:** Technical help. **Jourdan Christophe:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2021.104696>.

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