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ORIGINAL ARTICLE

Macrofauna accelerates nutrient cycling through litterfall in cocoa agroforestry systems

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Abstract This study aimed to better understand nitrogen (N), phosphorus (P), and potassium (K) cycling through litterfall in smallholder cocoa agroforestry systems and to assess if these nutrient flows can be measured using standard litterbags. Annual litter production, relative mass loss, and nutrient loss rates from cocoa leaf litter were evaluated in three farms in south-western Nigeria with and without macrofauna access. Litterfall was measured fortnightly close to the base of the cocoa tree and at the edge of the tree canopies from January 2020 to December 2021. Leaf litter decomposition rates were determined over 388 days in 2 mm mesh litterbags to exclude macrofauna and in frames open to the soil surface to allow macrofauna access. Concentrations of C, N, P, and K were measured in the remaining litter at 180, 244, 314, and 388 days after incubation. Annual estimates of litterfall (10.62 Mg DM ha^{-1}) did not significantly differ between the traps close to and away from the cocoa tree trunk. Nutrient cycling from litter was estimated at approximately 101 kg N, 5 kg P, and 89 kg K ha^{-1} $year^{-1}$. Relative litter decomposition rates (k) significantly differed between frames and litterbags. Macrofauna access significantly reduced the C:N ratio in the remaining litter and increased N and P loss from the litter layer by 28 and 69%, respectively. In conclusion, nutrient flows through litterfall are considerable, and N and P transfer rates to soil are likely underestimated in litterbag experiments that exclude macrofauna.

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Introduction

Cocoa (*Theobroma cacao* L.) in West Africa is mainly produced in low-input systems (Daymond et al. 2022; Wainaina et al. 2021), where farmers rely primarily on natural biogeochemical processes to maintain or improve the inherent soil fertility (Appiah et al. 1997; Duguma et al. 2001; Kenfack Essougong et al. 2020). Thus, the sustainability of cocoa production depends heavily on nutrient recycling within the plots.

Natural sources of nutrient inputs in low-input systems are atmospheric deposition, nitrogen fixation, and soil mineral weathering, all of which may be negligible in tropical environments (Hartemink 2005; Ossohou et al. 2020). Substantial amounts of nutrients are recycled and returned to the soil through litterfall. Based on studies from Malaysia, Venezuela, and Cameroon, Hartemink (2005) reported an estimated average of 84, 4, and 65 kg N, P, and K ha^{-1} $year^{-1}$ were recycled in low shade cocoa production systems. The accumulated litter progressively decomposes and releases nutrients, which can later be available for microbial and plant uptake. Therefore, the flow of nutrients through litterfall and litter decomposition plays a significant role in maintaining soil fertility and productivity of smallholder cocoa farms. The variability in cocoa litterfall and litter turnover rates has yet to be studied in detail. Hence, the contribution of litter decomposition to nutrient mineralization and soil nutrient availability is poorly understood in cocoa.

Only a few authors have studied cocoa litterfall in West Africa, where 70% of the world's cocoa is produced, and these have not addressed spatial and temporal variations of litterfall in detail. We found only two peer-reviewed papers from Ghana (Asigbaase et al. 2021a; Dawoe et al. 2010) and Nigeria (Muoghalu and Odiwe 2011; Ogunlade and Iloyanomon 2009), and a single one each from Côte d'Ivoire (Yao et al. 2021) and Cameroon (Saj et al. 2021). In these studies, annual litterfall was quantified, but without a clear and consistent link to the amounts of transferred nutrients released from decomposing litter.

Assessing spatiotemporal variation of litter stocks and the related nutrient flows in forests and tree crop systems is inherently challenging due to methodological limitations (Schroth and Sinclair 2003). Protocols for litterfall experiments vary strongly between studies: litter trap size, number and spatial distribution of litter traps, and duration of the experiment are not standardized, which affects the conclusions (Huang et al. 2018; Uriarte et al. 2015). In cocoa agroecosystems, the optimal position of litter traps relative to cocoa trees is not known. When specified, litter traps are set either randomly (e.g. Fontes et al. 2014) or at a fixed distance from the cocoa trees in systems where cocoa is planted at regular spacing (e.g. 0.5 m, Schneidewind et al. 2018). Regular shifting of litter traps may increase spatial representativity (Dawoe et al. 2010; Schroth and Sinclair 2003), but may be compromised by temporal litter fall variation. Cocoa trees are typically pruned into a "cup shape" (Tosto et al. 2022), which should reduce branch interlocking between adjacent trees. This shape likely results in a gradient in litterfall from the stem of the cocoa trees to the edge of the canopy. In practice, it is unclear how heterogeneous the litter is under cocoa trees, meaning that the positioning of the litter trap may have a large effect on the amount of litter trapped. The extent to which the position of the litter trap influences the accuracy of litterfall estimation is unknown, especially in traditional cocoa agroecosystems characterized by irregular planting patterns.

Nutrient mineralization is tightly linked to litter decomposition, which is affected by various soil organisms, which are broadly classified according to their size: macro- (larger than 2 mm), meso- (from 100 µm to 2 mm), and micro-fauna (less than 100 µm) (Centenaro et al. 2018). Macrofauna is diverse and abundant in soils under natural ecosystems and no-till agricultural systems (Maria de Aquino et al. 2008; Smith et al. 2008); this is also expected under cocoa. Macrofauna significantly contributes to litter fragmentation, ingestion, and mixing with soil particles, but they also control microbial communities and activities (Lavelle et al. 2006), thus affecting litter decomposition and nutrient mineralization rates. However, to our knowledge, their relative contribution to litter transformation and nutrient release in cocoa has yet to be quantified.

The choice of litterbag mesh size determines which organisms can access the substrate. Standard

incubation trials partially or totally exclude macrofauna. The usual size of litterbag mesh varies from 0.5 to 2 mm (Li et al. 2022; Paudel et al. 2015), which excludes macrofauna (e.g. beetles, earthworms, ants, and termites) normally present in cocoa litter (da Silva Moço et al. 2009). Mesh sizes reaching 10 mm are used in other systems (Lecerf 2017), but those were not included in previous cocoa litter studies. Therefore, previous cocoa litter decomposition studies (Bai et al. 2022; Muoghalu and Odiwe 2011; Sari et al. 2022) have not accounted for macrofauna activity and their role in cocoa litter decomposition and nutrient release is largely unknown. A significant effect of macrofauna on litter decomposition and nutrient release would call for a review of the interpretation of previous estimations.

This study aimed to better understand nutrient cycling through litterfall in smallholder cocoa farms in south-western Nigeria. The first objective was to evaluate differences in annual amounts of litterfall close to and away from the trunk of cocoa trees. The second objective was to quantify the effect of macrofauna on the rate of cocoa leaf litter disappearance from the litter layer and on changes in N, P, and K concentrations of the remaining litter. We hypothesized that (1) litter fell more abundantly close to the stem than at the edge of the canopy, and (2) macrofauna increased the litter mass loss rate (disappearance) as well as N and P loss from the cocoa leaf litter (nutrient removal rates). An experiment was conducted in three smallholder cocoa fields that involved litterfall measurements over two consecutive years, and an incubation trial of cocoa leaf litter with and without access of macrofauna over one year.

Materials and methods

Study area and site description

The study area falls in the sub-humid agroecological zone characterized by average monthly temperatures in the range of 23.5 °C (September) to 27.7 °C (January) and 45. 5–97.6% relative humidity (RH). The annual rainfall is unimodal with a long rainy season and a total between 1377 and 1965 mm, while the dry season runs from December to March. A dry spell occurred in August during the first year of data collection.

The experiment ran from January 2020 to December 2021 in south-western Nigeria, in three farmer-owned cocoa farms of about 1.5 ha each (hereafter named "Ago-Owu", "Akowonjo-Akoko", and "Ijebu-Itele") that were 100–300 km apart. The major soil types in all selected fields were lixisols (Hengl et al. 2021). The texture was sandy loam to sandy clayey loam (Table 1). The cocoa trees were about twenty years old, and cocoa was established on previous forest land. The farms are representative of low-shade cocoa agroforestry systems managed by smallholders in the region (Sonwa et al. 2014, 2019), and cocoa trees are pruned once or twice a year. No fertilizers were applied in any of the farms since the cocoa was established, and all weeds and tree residues were left to rot. Oil palms (*Elaeis guineensis* Jacq.), cola trees (*Cola nitida* Schott & Endl.) and a few forest-remnants form the upper canopy (approximately 8 m), while cocoa and *Citrus* spp, share the lower canopy (approximately 4 m). The shade trees are not managed. Other field characteristics are shown in Table 1.

Data and observations

In each cocoa farm, all observations were made in two plots of 21 m × 21 m established 30–50 m apart (Fig. 1). Interpolated monthly rainfall and daily air temperatures for the three sites were obtained from the National Aeronautics and Space Administration (NASA) agroclimatology predictor (https://power.larc.nasa.gov/data-access-viewer/).

The cocoa tree aboveground biomass was estimated after measuring the diameters of all cocoa trees at 30 cm aboveground and using a cocoa-specific allometric equation (1) developed for nearby cocoa farms of similar production systems in Oyo state (Ajibona 2023).

$$AGB = 0.055D^{2.267} \quad (1)$$

where AGB (kg) is the aboveground biomass of the cocoa tree, and D (cm) is the stem diameter measured at about 30 cm above the soil surface.

The canopy cover, which provides an indirect estimate of the potential light environment under the canopy, was estimated based on hemispherical photographs taken in November 2020 at 1 m aboveground, under the canopy of five randomly selected cocoa trees. The images were processed using default

Table 1 Mean values ± standard deviation of topsoil properties (0–30 cm) of the study sites, the cocoa farm characteristics, and the initial litter chemical properties of the study sites

Parameters	Location		
	Ago-Owu	Akowonjo-Akoko	Ijebu-Itele
Coordinates (decimal degrees)	4.2031 °E, 7.1482 °E	5.6203 °E, 7.4383 °E	4.3667 °E, 6.9833 °E
Elevation (m)	272	328	295
	Soil properties		
Sand (g kg^{-1})	680 ± 0.0	730 ± 7.1	750 ± 4.2
Silt (g kg^{-1})	90 ± 1.4	90 ± 1.4	90 ± 1.4
Clay (g kg^{-1})	230 ± 1.4	180 ± 5.7	160 ± 2.8
Bulk density (Mg m^{-3})	1.11 ± 0.2	1.15 ± 0.1	1.12 ± 0.1
pH (H_20)	6.85 ± 0.1	6.20 ± 0.3	6.70 ± 0.7
Organic C (g kg^{-1})	11.80 ± 0.7	8.53 ± 0.7	9.60 ± 2.2
Total N (g kg^{-1})	1.21 ± 0.0	0.79 ± 0.1	0.86 ± 0.1
Available P (mg kg^{-1})	3.51 ± 1.4	2.80 ± 1.4	0.82 ± 0.4
Exchangeable P (cmol kg^{-1})	0.18 ± 0.04	0.14 ± 0.01	0.15 ± 0.01
Exchangeable Ca (cmol kg^{-1})	6.47 ± 0.79	5.25 ± 0.49	1.63 ± 0.45
Exchangeable Mg (cmol kg^{-1})	0.87 ± 0.01	0.53 ± 0.01	0.40 ± 0.08
	Tree community characteristics		
Age of plantation (years)	18	15	23
Shade tree density (trees ha^{-1})	27	8	56
Cocoa tree density (trees ha^{-1})	985	1087	1162
Cocoa stem diameter (cm) at 30 cm	14.2 ± 2.79	18.1 ± 3.66	13.8 ± 2.81
Cocoa canopy diameter (cm)	221 ± 47.7	337 ± 62	154 ± 61.1
Cocoa tree height (cm)	488 ± 79.4	407 ± 70.9	440 ± 64.7
Cocoa canopy cover (%)	77.70 ± 5.51	76.80 ± 6.15	76.7 ± 3.03
	Initial litter quality		
C concentration (g kg^{-1})	610 ± 1.27	555 ± 64.14	637 ± 1.04
N concentration (g kg^{-1})	10.80 ± 0.00	9.25 ± 0.17	11.15 ± 0.87
P concentration (g kg^{-1})	0.65 ± 0.06	0.50 ± 0.00	0.50 ± 0.00
K concentration (g kg^{-1})	11.80 ± 0.12	5.80 ± 0.23	11.30 ± 0.00
C:N (g g^{-1})	56.44 ± 0.12	59.96 ± 5.81	57.34 ± 4.36
C:P (g g^{-1})	943 ± 81.83	1111 ± 128.29	1273 ± 2.08

settings of the Gap Light Analyzer (GLA) software (Frazer et al. 1999).

Litterfall

Litterfall was estimated based on the standard litter trap method (Anderson and Ingram 1993). Within each plot, five cocoa trees were randomly selected, and paired litter traps (0.8 m × 0.5 m) were placed: one at 20 cm from the cocoa tree trunk (hereafter "close"), and the other half-way between the tree trunk and an adjacent cocoa tree trunk, at an average distance of 1.38 ± 0.5 m from the stem (hereafter "away"). The away litter traps fell within the area of interlocking branches of two adjacent cocoa trees. The design led to 10 litter traps per plot, thus with five traps per position under the canopy. Since the experiment focused on cocoa litter, all litter traps were set regardless of the position of shade trees. However, litter trap positions never fell directly under the canopy of a shade tree. Litterfall was collected fortnightly from January 2020 to December 2021. Due to travel restrictions at the onset of the Covid-19 pandemic and at times of civil unrest, we were unable to collect litter from April 2020 to June 2020 in any of the farms and from March 2021 to May 2021

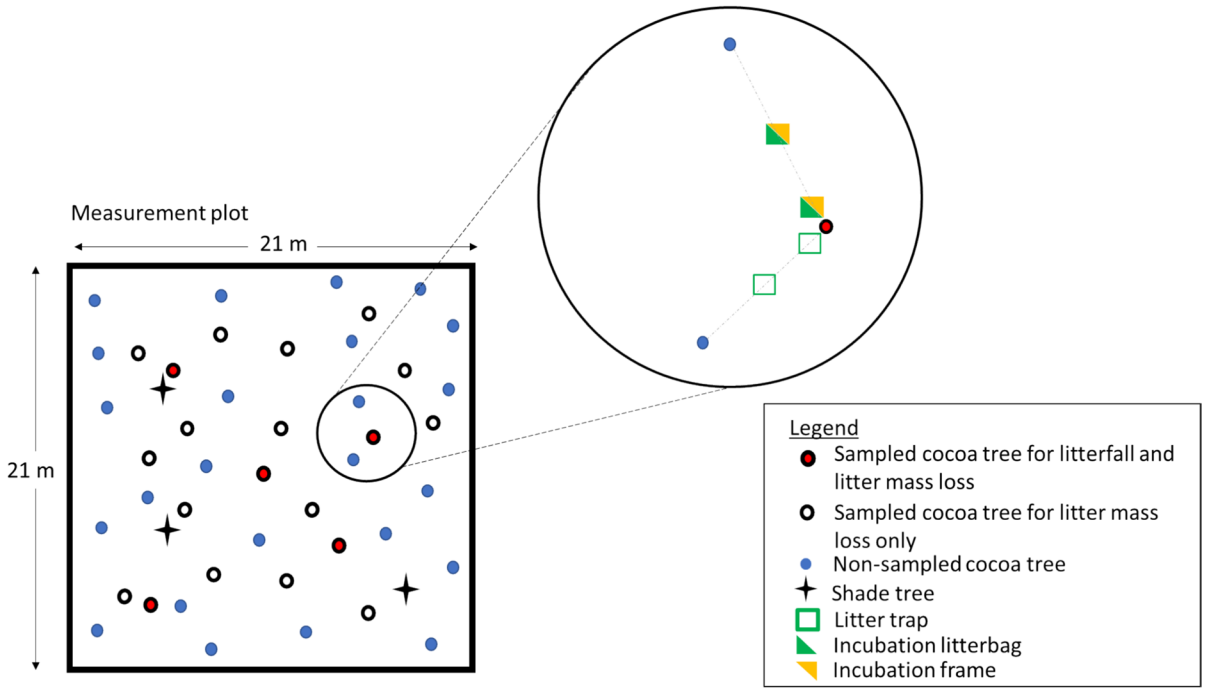

Fig. 1 A typical layout of an experimental plot in a farmer's cocoa farm

in Akowonjo-Akoko, where the 2021 civil conflicts were more intense, and the farm was not accessible. At the end of these periods, the entire litterfall was quantified.

All litter samples extracted from the litter traps were oven-dried at 65ºC to constant mass and sorted into cocoa leaves, shade-tree leaves, and other fragments (mostly twigs). Each component of the litterfall, i.e. cocoa leaf litter, shade-tree leaf litter, and other fragments, was aggregated per year for analysis.

Soil and litter analyses

Soil samples from 0 to 30 cm depth (where 90% of cocoa roots are located, Borden et al. 2020) were randomly collected at ten positions in each plot using a soil auger. These samples were pooled for each farm, air-dried, thoroughly mixed, and subsampled for physical and chemical analysis. Soil texture was determined by the hydrometer method (Dane et al. 2002). Soil pH was determined in 1:2.5 (w/v) soil to water suspension (McLean 1983). Exchangeable cations, Ca^{2+}, Mg^{2+}, and K^{+} were extracted by the Mehlich-3 procedure. Cation concentrations were determined by atomic absorption spectrophotometry (AAS) and phosphate P content by the molybdate blue procedure according to the Olsen method. Soil and litter organic carbon contents were determined using the Walkley–Black chromic acid wet oxidation method (Nelson and Sommers 1996). Total nitrogen content was determined by the Kjeldahl digestion method using concentrated sulphuric acid and sodium copper sulphate catalyst mixture and distillation in boric acid. Soil bulk density was determined using two randomly sampled cores of 100 cm^3 per plot (Grossman and Reinsch 2002).

Concentrations of C, N, P, and K in cocoa leaf litter were determined after pooling samples per farm (Table 1). Total N, P, and K contents in cocoa leaf residues were analysed with Kjeldahl method, molybdate blue colorimetry, and AAS after digestion, respectively. Carbon and nutrient flows through cocoa leaf litterfall were estimated annually by multiplying concentrations estimated in freshly fallen cocoa leaf litter (collected in December 2019) with the dry mass of cocoa leaf litterfall aggregated per year.

Cocoa leaf litter disappearance and nutrient losses

Cocoa leaf litter mass loss and nutrient loss from the litter layer were assessed in situ through the incubation method (Anderson and Ingram 1993). One plot per farm was randomly selected for this experiment. Forty grams of freshly senesced cocoa leaves were collected in the same plots in December 2019 and enclosed either in 40 cm × 30 cm litterbags of 2 mm mesh size or placed directly on the soil surface within a frame of equal size covered by 2 mm mesh to prevent mixing with foreign materials such as subsequent litterfall or disturbance by wind and animals. The initial mass of cocoa leaves (40 g per sample) was set to simulate a total leaf litter mass of 3300 kg ha^{-1}, corresponding to the average standing litter mass measured in 0.8 m × 0.5 m quadrats in December 2019 in adjacent plots; we used a total of ten quadrats per duplicate in each site. Before the incubation, the soil surface was cleared from pre-existing residues and the frames and litterbags were gently placed, labelled, and fixed with bamboo pegs to avoid undesired movements. Litterbags and frames were placed side by side. A total of forty sets of litterbags and frames were placed per plot, each under a randomly selected cocoa tree, and at two positions relative to the canopy. Between January 2020 and January 2021 and starting at 14 days after incubation (DAI), one set of litterbag and frame was randomly retrieved at 14-day intervals during the rainy season and at 21-day intervals during the dry season.

The residues from the litterbags and frames were oven-dried, soil particles were brushed off, and their dry weight was determined. Cocoa leaf litter mass loss data was used to estimate the relative decomposition constant rate k for litterbags ($k_{\text{with macrofauna}}$) and for frames ($k_{\text{without macrofauna}}$), based on a first-order exponential decay model (2), Olson 1963):

$$m_t = m_i e^{-kt} \quad (2)$$

where m_i and m_t are the initial and residual cocoa leaf litter mass at t days after incubation (DAI) respectively, and k is the estimated parameter.

Leaf litter was analysed to determine C, N, P, and K concentrations, according to procedures described in the "Soil and litter analyses" section. For the chemical analyses, one sample per plot was taken from the residues retrieved from litterbags and frames at 0, 180, 248, 314, and 388 DAI. The amount of C, N, P, and K in the litter residues was calculated from the elemental concentrations and the dry mass of the residues. The effect of macrofauna on C and N, P, and K loss was estimated at 180, 248, 314, and 388 DAI, by comparing the amount of nutrients in the residues (relative to the initial amount at start) between litterbags and frames. The effect of macrofauna on the quality of the remaining litter was assessed by evaluating nutrient ratios (namely C:N, C:P, and N:P) in the residues.

Statistical analyses

Annual amounts of cocoa leaf litterfall collected close to- and away from- the cocoa tree stems were analysed using a generalised linear mixed-effect model (GLMM). Fixed-effect factors were the distance to the stem (close vs away) and year, without interaction. A first analysis indicated the interaction was not significant, so it was excluded from the final analysis (Table 4). The random-effect factors included in the model were the farms, plots within farm, and the sampled trees within each plot. The two other components of the total litterfall, i.e. shade tree leaves and other fragments, were analysed in the same way. Annual amounts of C, N, P, and K that flow through cocoa leaf litterfall were analysed using descriptive statistics.

The relative decomposition rates of cocoa leaf litter (k) were estimated as per equation (2), i.e. by calculating the slope of the relationship between time (t) and the log-transformed residual mass of litter (m_t/m_i). The values of $k_{\text{without macrofauna}}$ and $k_{\text{with macrofauna}}$ were estimated for each plot within each farm using linear regression, and the six values (2 treatments and three sites) were compared through analysis of variance (ANOVA) after verifying gaussian distribution of residuals and homoscedasticity through Levene's test. Additionally, Shapiro Wilk' tests were used to assess the normality of the response variable.

The C, N, P, and K concentrations in the residual cocoa leaf litter, the nutrient ratios (C:N, C:P, and N:P), and the relative loss were analysed with linear mixed-effects models, considering the sampling dates (0, 180, 248, 314, and 388 DAI), the effect of litter trap mesh size on macrofauna access, and their interaction as fixed-effect factors. Random-effect factors were the farms and plots within each farm.

Differences between litterfall collected close and away, and between $k_{(without\ macrofauna)}$ and $k_{(with\ macrofauna)}$ were evaluated with a Wald-type F test. All analyses were performed in R (R Core Team 2013). The homoscedasticity of model residuals was verified graphically, using the *DHARMa* package (Hartig 2019).

Results

Carbon and nutrient flows through litterfall

On average, 10.62 ± 3.58 Mg DM ha^{-1} of litterfall was recorded across all sites. Approximately 93% of this litterfall was senescent cocoa leaves. Shade tree leaves and other fragments (mostly twigs) contributed very little to the litter under the cocoa canopy (Table 2). For all fractions (cocoa leaves, shade tree leaves, and other fragments), there was no significant difference in the amounts of litterfall collected close to and away from the cocoa trees ($P > 0.05$). Within-farm and, to some extent, within-plot variations were smaller than between-farm variation, accounting for 3, 16, and 59% of total variation, respectively. Differences between the two years were not significant ($P > 0.05$). Monthly variations were large as litterfall increased when rainfall declined in the drier period of the year (Fig. 2).

The annual transfer of cocoa leaves to the litter layer corresponded to a flow of 5.87 ± 1.93 Mg C ha^{-1} year^{-1}. The estimated N and K flows through cocoa leaf litterfall were considerable: 101 ± 32 kg N ha^{-1} year^{-1} and 89 ± 27 kg K ha^{-1} year^{-1}. In contrast, the amount of P transferred through cocoa leaf litterfall was small, with an average of 5 ± 2 kg P ha^{-1} year^{-1} (Fig. 3).

Cocoa leaf litter disappearance

Cocoa leaf litter disappearance rate was significantly greater when macrofauna could access the litter than without macrofauna access: $k_{(\text{without macrofauna})}$, estimated at 0.0023 day^{-1}, and was 1.35 times larger than $k_{(\text{with macrofauna})}$ (0.0017 day^{-1}, and $P < 0.05$). Cocoa leaf litter mass decreased by 54% in the litterbags and the additional mass loss attributed to the access by macrofauna was about 8% at 388 DAI (Fig. 4).

Stoichiometry of the decomposing cocoa leaf litter

Macrofauna also affected the quality of the decaying cocoa leaf litter. Carbon concentrations of the remaining cocoa leaf litter slightly decreased from 60% at the beginning of the incubation (0 DAI) to about 55% at 248 DAI, with no significant differences between litterbags and the open frames ($P > 0.05$). However, at 314 DAI and 388 DAI, C concentrations were lower in the frames than in the litterbags ($P < 0.01$, Fig. 5).

Nutrient loss from decomposing cocoa leaf litter

The release patterns of carbon and nutrients that were not lost from cocoa leaf litter showed similar rates, with large differences in relative loss at 180, 248, 314 and 388 DAI. Between the start and the end of the incubation period, relative amounts of C, N, and K were reduced by 56%, 33%, and 90%, respectively (Fig. 6). Amounts of P in the remaining litter increased two-fold in Akowonjo-Akoko and remained nearly constant in the two other sites. When data from the three sites were combined, an overall increase in P amounts was found ($P < 0.001$). The increase in P contents in the remaining cocoa leaf litter was less pronounced when macrofauna had access, especially at 314 DAI ($P < 0.05$) and at 388 DAI ($P < 0.001$).

Table 2 Means ± standard deviation of annual litterfall mass (Mg ha^{-1}) estimated close to- and away from- the cocoa tree stems across years and study sites

Position of the litter trap	Quantities of litterfall (Mg ha^{-1})			
	Cocoa leaves	Shade tree leaves	Other fragments	Total
Close	10.04 ± 3.47 (92.4)	0.07 ± 0.27 (0.5)	0.75 ± 0.60 (7.2)	10.83 ± 3.57
Away	9.70 ± 3.48 (93.1)	0.07 ± 0.20 (0.6)	0.63 ± 0.53 (6.4)	10.40 ± 3.59

Figures in brackets are the relative contribution (%) to the total. No significant differences were observed between litterfall components collected in the two litter trap positions

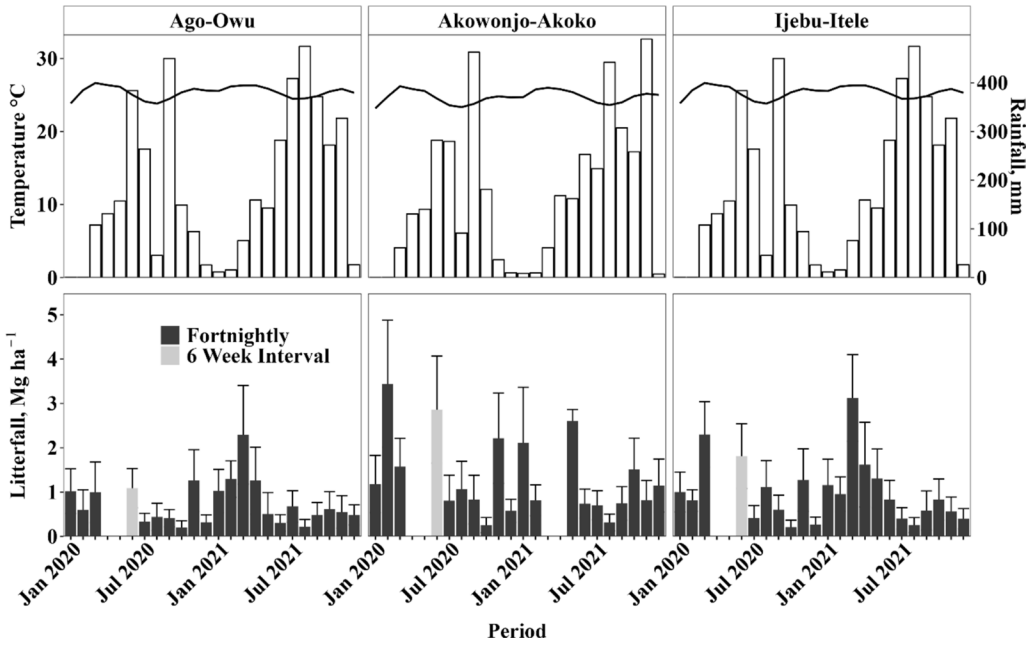

Fig. 2 (Upper panels) Monthly rainfall (bars) and average temperature (lines), and (lower panels) amounts of litterfall (mean ± standard deviation) in three smallholder cocoa farms in south-western Nigeria. Fortnightly sampling from March–May 2020 is shown in dark-gray, the first sampling after the February-May 2021 period of civil unrest is shown in light-gray bars

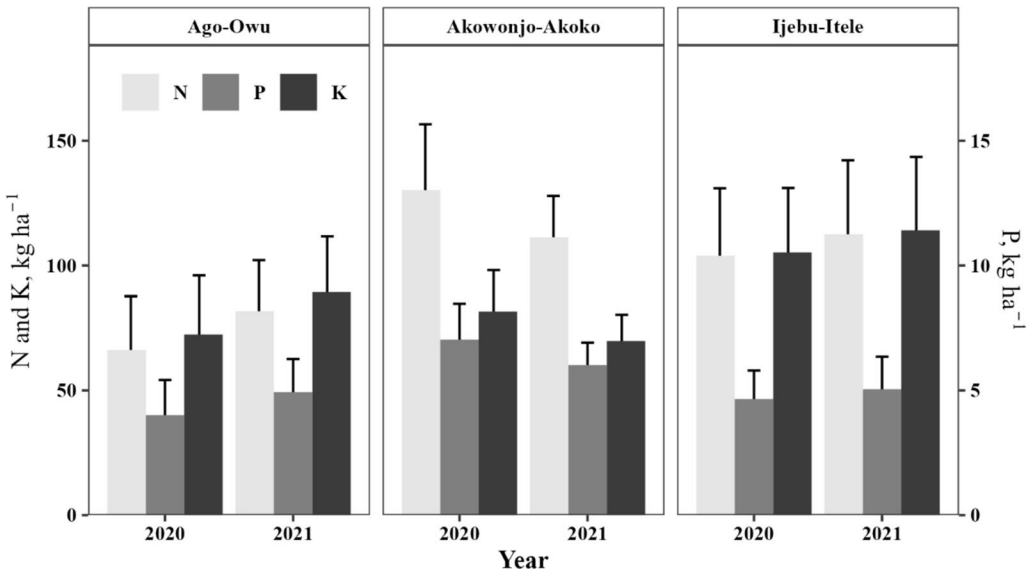

Fig. 3 Amounts (mean ± standard deviation) of N, P, and K estimated in annual cocoa leaf litterfall in three smallholder cocoa farms over two years in south-western Nigeria

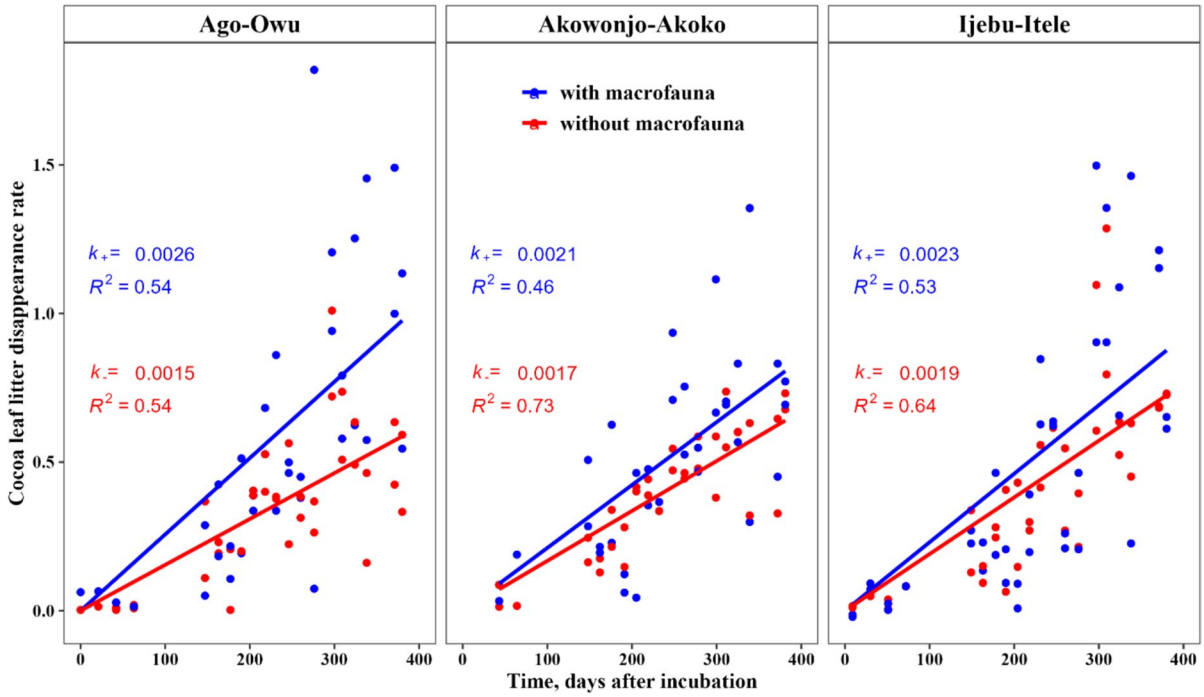

Fig. 4 Cocoa leaf litter disappearance rate from the litter layer in three smallholder cocoa farms in south-western Nigeria. The legend refers to the sampling methods, with frames and litterbags corresponding to "with macrofauna" and "without macrofauna"

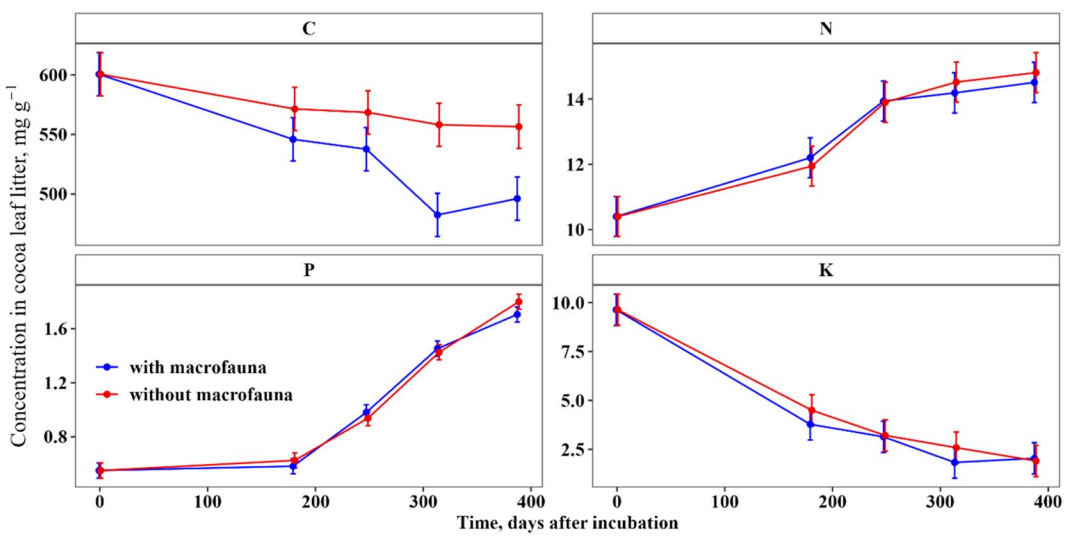

Fig. 5 Estimates (±standard error) of C, N, P, and K concentrations in decomposing cocoa leaf litter enclosed in litterbags (without macrofauna) and frames (with macrofauna) in three smallholder cocoa farms in south-western Nigeria. The legend refers to the sampling methods, with frames and litterbags corresponding to with macrofauna and without macrofauna respectively

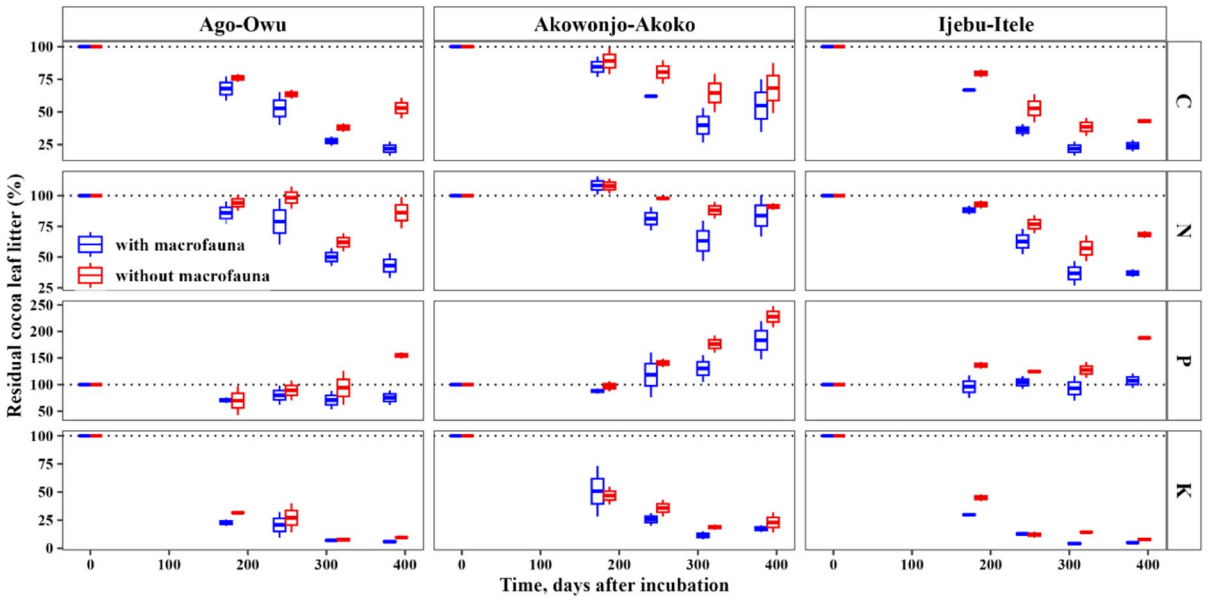

Fig. 6 Carbon and nutrient loss from decomposing cocoa leaf litter in three smallholder cocoa farms in south-western Nigeria. The legend refers to the sampling methods, with frames and litterbags corresponding to with macrofauna and without macrofauna respectively

More than 64% of K was lost from the cocoa leaf litter at 180 DAI, irrespective of macrofauna access ($P > 0.05$). Nitrogen loss was gradual, and significantly larger losses were observed when macrofauna had access. At 180 DAI, 5% N was lost with no effect of macrofauna ($P > 0.05$). At 248 and 388 DAI, 10 and 19% of N were lost without macrofauna access, respectively, against 27 and 47% when macrofauna had access ($P < 0.05$).

Access of macrofauna did not affect the observed gradual changes in N, P, and K concentrations of the cocoa leaf litter during incubation ($P > 0.05$). As a result of declining C concentrations and increasing N and P concentrations, the C:N and C:P ratios decreased over time ($P < 0.001$). The N:P ratios also declined ($P < 0.001$) because C:P ratios declined more drastically than C:N ratios (Table 3). However, the C:N ratios declined more rapidly in the frames than in the litterbags ($P < 0.01$). At 388 DAI, the average C:N ratios were estimated at 34.4 with, and 38.1 without access of macrofauna, respectively.

Discussion

This study highlighted three main results: (1) there is a large amount (10.62 Mg ha^{-1}) of dry matter recycled annually through litterfall, however, with large variations between farms, and between trees in the same farm; (2) considerable amounts of carbon and

Table 3 Change in stoichiometry of decomposing cocoa leaf litter with or without access of macrofauna

Ratio	Macrofauna access	Time (DAI)				*P*-value for ANOVA F-test		
		180	248	314	388	Time	Macrofauna	Interaction
C:N	With	44.8	38.9	34.2	34.4	$P < 0.001$	$P < 0.01$	ns
	Without	47.9	41.5	38.8	38.1			
C:P	With	967	568	335	290	$P < 0.001$	ns	ns
	Without	975	623	397	311			
N:P	With	21.5	14.5	9.9	8.52	$P < 0.001$	ns	ns
	Without	20.4	15.2	10.3	8.25			

Non-significant differences ($P > 0.05$) are denoted ns, and time is expressed in days after incubation (DAI)

nutrients (101 kg N ha^{-1}) are present in cocoa leaf litterfall in these cocoa farms; however only a small fraction of N and P is released within a year after litter fall; (3) macrofauna access to the litter resulted in 8% additional mass loss of leaf litter per year when compared with incubation in standard litterbags, this increased the estimated N and P loss from the litter layer by 28 and 69%, respectively.

Contribution of cocoa leaf litterfall to nutrient recycling in cocoa agroforestry systems

Results from this study suggest that 34–186 kg N ha^{-1} $year^{-1}$, 37–175 kg K ha^{-1} $year^{-1}$, and 2–10 kg P ha^{-1} $year^{-1}$ were likely transferred from cocoa trees to the soil through litterfall. For N and K, these estimates align with the ranges (84–175 kg N ha^{-1} $year^{-1}$ and 16–124 kg K ha^{-1} $year^{-1}$) found in the review by van Vliet and Giller (2017). Observed *P* contents in litterfall and, hence, flows to soil were smaller than observed in other studies (5.8–17 kg P ha^{-1} $year^{-1}$), which indicated that the cocoa trees in this study had less *P* in their senescent leaves. The initial *P* concentration in the senescent cocoa leaves (0.55 mg g^{-1}) was substantially lower than the reported values of 1.2 ± 0.5 mg g^{-1} (Hartemink 2005), probably reflecting the very poor *P* status of the soils (Table 1). Recorded amounts of annual litterfall were close to estimates (5-10 Mg DM ha^{-1} $year^{-1}$) for various cocoa production systems in Côte d'Ivoire (Yao et al. 2021), Cameroon (Saj et al. 2021), and Ghana (Dawoe et al. 2010), but larger than estimates from Brazil (Fontes et al. 2014), Mexico (Perez-Flores et al. 2018), and Indonesia (Sari et al. 2022). The differences between studies are likely due to climate, age of cocoa trees, planting materials, production system, and also management including the pruning regime (Andivia et al. 2012; Asigbaase et al. 2021b; Farooq et al. 2022; Giweta 2020; Qiu et al. 2023). Shade tree density and diversity were not accounted for in this study, which was justified by the observed low density of shade trees. In addition, their contribution to soil organic matter (SOM) and cocoa nutrition is presumably marginal and limited to the immediate vicinity of the closest trees (Kaba et al. 2019). Although shade trees can affect cocoa production within a radius of 11 m (Saj et al. 2023), mainly the cocoa trees in the vicinity of shade trees will be severely affected by resource competition for light and nutrients (Schmidt et al. 2022). In this study, the litter trap in which the contribution of shade tree leaves was largest received an amount equivalent to 0.95 Mg DM ha^{-1} $year^{-1}$. Cocoa leaf litterfall near the stem was not different from litterfall at the edge of the canopy. This suggests that the position of the litter traps does not affect the measurements, for farms with cocoa tree densities comparable to those in this study (approximately 1000 trees ha^{-1}). West African cocoa farmers usually adopt tree densities in the range of 1000–2500 trees ha^{-1} (Sonwa et al. 2019). In contrast, lower cocoa tree densities (about 568 trees ha^{-1}) are preferred in fine-flavoured cocoa agroforestry systems found in Central America (Somarriba et al. 2013). In farms characterized by lower densities and/or large gaps between Eucalyptus trees (e.g. due to severe mortality and insufficient replanting), significantly smaller amounts of litterfall may be found away than close to the stems (Barnes et al. 2011). Accurate estimation of litterfall under such conditions will require accounting for area loss (large gaps without cocoa trees) and incomplete canopy closure. The amount of litterfall in this study varied substantially, with notable differences observed both between farms and between individual trees within the same plot. In contrast, other cocoa systems observed minimal litterfall contributions from associated tree species. However, cocoa leaf litter is generally considered recalcitrant, while the litter from associated trees is often less recalcitrant. This difference in litter quality can accelerate the decomposition of cocoa litter when mixed with that of associated trees. The heterogeneity in litterfall causes variability in macronutrient availability in forest soils (Xia et al. 2015). However, to improve the accuracy and representativeness of litterfall measurements, increasing the number of litter traps per plot and adhering to rigorous sampling protocols is essential. Previous studies typically used a median of three litter traps per plot (Dawoe et al. 2010; Saj et al. 2021; Yao et al. 2021; Sari et al. 2022). In this study, we used ten litter traps, five near the base of cocoa trees and five farther away. For instance, increasing the number of traps from three to ten can halve the standard error of estimated litterfall (data not shown).

Nutrient-specific loss rates from the cocoa litter

In this study, large amounts of N and P were immobilized in the litter layer after one year. Our results also suggested that microbial respiration occurred throughout the incubation but was only strengthened by macrofauna activity towards the second half of the experiment, probably due to seasonal rainfall patterns. Phosphorus was strongly immobilized within the litter layer. Potassium (K) was rapidly lost from both frames and litterbags, whereas N was first immobilized within the litter, and subsequently released and lost during the second half of the year. Greater losses of N and P were observed from frames than from litterbags towards the end of the experiment. Differences in nutrient loss rates from decaying plant materials have been recognised and are likely related to the stoichiometry of the substrate and the demand of soil microbial biomass (Čapek et al. 2021; Murungu et al. 2011).

In this study, more than half of the N and P were still immobilized in the litter layer after one year. Litter decomposition rates can be measured in various ways, including the mass balance method (combined measurements of standing litter stock and inputs through litterfall), the mass loss method involving incubation in litterbags, litterbaskets or in tethered litter, or through respiration measurements (Berg and McClaugherty 2014; Nadelhoffer and Blair 1999; Schroth and Sinclair 2003). Each measurement method represents decomposition processes differently (microbial catabolism, physical fragmentation and leaching). Hence, the selection of the appropriate method depends on the objective of the study. In cocoa, the two most used methods are the mass balance and the mass loss (Kaba et al. 2021; Mohammed et al. 2019; Rojas-Molina et al. 2021; Yao et al. 2021). It is challenging to compare the estimated decomposition rates because of variations in substrates (cocoa leaves, twigs, shade tree leaves, and various combinations), protocols, analytical procedures, and calculated indices. Nevertheless, the mean residence time (MRT), defined as the "time to replace the equilibrium amount of C by the (annual) supply" (de Willigen et al. 2008), is a common measure of the average time of any particle (e.g. a freshly fallen leaf) in a particular state (the litter layer). Mean residence time (MRT) of C and major macronutrients have been estimated in the cocoa litter layer. For instance, in nine cocoa agroforestry systems assessed in Brazil, Fontes et al. (2014) found that N, P, and K had similar MRTs (about 1.5, 1.2, and 1.4 years, respectively). In contrast, this study found a smaller MRT for K than N and Asigbaase et al. (2021b) also measured nutrient release from decaying cocoa leaf litter in Ghana, and found no residual K and less than 10% residual P after one year, and approximately 20% residual N after nine months. The differences between these studies are probably related to the diversity of systems including pedoclimatic conditions, germplasm and crop management, and methods used, including the timing of the experiment relative to rainfall patterns (Cusack et al. 2009; Yahdjian and Sala 2008), the macrofauna community and environmental conditions affecting litter decomposition (Ball et al. 2022; Li et al. 2021).

The role of macrofauna in litter mass loss and nutrient release

In this study, access by macrofauna was associated with a relatively small but significant additional mass loss (8%) after one year of litter decomposition under cocoa trees. Macrofauna access exerted a greater effect on N and P dynamics at the litter-soil interface. The conventional litterbag method (with mesh size < 2 mm) underestimates decomposition rates. The litter mass loss associated with mesofauna and macrofauna can reach 50% in natural ecosystems such as forests and grasslands (Frouz et al. 2015; Jo et al. 2019; Liu et al. 2021; Long et al. 2021), where the effect of macrofauna on litter mass loss increases over time (Pompermaier et al. 2021; Schädler and Brandl 2005). However, certain arthropods slow down the decomposition rate of composted leaves (Ball et al. 2022). Comminution and assimilation by macrofauna are the main drivers of litter mass loss (Frouz 2018). However, relations between litter mass loss due to macrofauna and nutrient loss from the litter layer are not linear (Warren and Zou 2002), and the preferential degradation of cellulose and lignin could explain the delayed release of N (Xu et al. 2023). A singular result was the increasing P concentrations and

calculated P amounts in the remaining litter that was observed at Akowonjo-Akoko. This is counter-intuitive because P amounts remain constant over time when completely immobilized in microbial biomass or decline because of loss from the litter layer. An increase in P amounts was also observed for leaf litter of cocoa and two shade tree species in a previous study (Bai et al. 2022). The mechanisms driving such an increase in P amounts in litter are still unknown and deserve to be further examined. It has been suggested that nutrients immobilized in decomposer biomass may not only originate from the decomposing litter, but also from the soil, especially when fungi and filamentous bacteria are major contributors to litter decomposition (Martins et al. 2021; Moore et al. 2008).

Conclusion

A better understanding of nutrient cycling in tropical tree cropping systems is essential to evaluate how nutrient management may affect such systems. With substantial litterfall (10.62 ± 3.58 Mg of dry matter ha^{-1}) and nutrient recycling, mature cocoa trees exhibit significant internal nutrient flows. This study found that cocoa litterfall allows the recycling of about 100 kg N ha^{-1}, 5 kg P ha^{-1}, and 89 kg K ha^{-1} in the examined cocoa agroforestry systems. Macrofauna significantly increased litter N and P loss rates from the litter layer but not K loss rates. Therefore, standard litterbag experiments in cocoa likely underestimate N and P loss rates and hence total losses. The study also showed that the two tested littertrap positions under the edge of the canopy did not affect litterfall estimates.

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Author contributions O. Oyedele and Deo-Gratias J. M. Hougni conducted the study including literature search, data analysis and manuscript writing; A. G. T. Schut, L. S. Woittiez, L. Rusinamhodzi, M. O. Ogunlade, S. Hauser and K. Giller contributed to drafting the proposal and supervision. A. G. T. Schut made significant input in data analysis, while K. Giller; Deo-Gratias J. M. Hougni; S. Hauser; M. O. Ogunlade developed the study design and O. Oyedele did the data collection. All authors reviewed the manuscript.

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Data availability The datasets analysed for the current study are available from the corresponding author on reasonable request.

Code availability https://github.com/BB1464/Manuscript

Declarations

Conflicts of interest The authors declare no competing interests.

Ethical approval Not Applicable.

Consent to participate Not Applicable.

Consent for publication Not Applicable.

Appendix

See Table 4.

Table 4 Results of the analysis of variance with the mean squares and significance of the litter trap position, year, and their interaction on the amounts of litterfall components collected in the two litter trap positions over two years

Factors	Cocoa leaves	Shade tree leaves	Other fragments
Litter trap Position	0.0198^{ns}	0.3406^{ns}	2.4328^{ns}
Year	0.0352^{ns}	1.0719^{ns}	18.2709^{***}
Litter trap Position × Year	0.0171^{ns}	0.3426^{ns}	2.4768^{ns}

ns = No significant difference at $P \leq 0.05$, *** = significantly different at 0.001

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