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REGULAR ARTICLE

Balancing litterfall and decomposition in cacao agroforestry systems

Rika Ratna Sari · Danaë M. A. Rozendaal · Danny Dwi Saputra · Kurniatun Hairiah · James M. Roshetko · Meine van Noordwijk

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Abstract

Backgrounds and aims Litter protects the underlying soil, depending on litterfall and decomposition, but dynamics of the standing litter stock in agroforestry systems remain poorly understood. We aimed to unravel effects of litter quality, temporal patterns, microclimate, and a possible home-field advantage (HFA) on standing litter dynamics across a land-use gradient.

Methods We quantified litterfall, the standing litter stock, and microclimate during a year in (remnant) forest, cacao-based simple and complex agroforestry, cacao monocultures, and annual crops in a cacao producing area in Indonesia. We conducted a reciprocal litter transfer experiment, and tested decomposition rates of pruning residues. Standing litter stocks during the year were estimated from monthly litterfall and decomposition rates.

Results Variation in litter quality influenced decomposition rates more strongly than variation in microclimate or HFA. Lower litter quality in complex agroforestry and in the cacao monoculture decreased the decay rate compared to simple agroforestry systems; mean litter residence time was over a year. Mixing high- and low-quality material in pruning residues modified the decomposition rate, soil C and N changes, offering options for targeted management of soil protection and nutrient release.

Conclusions The seasonal patterns of litterfall and relatively slow decomposition rates supported permanence of the litter layer in all cacao production systems, protecting the underlying soil.

Keywords Litter quality · Standing litter · Decomposition · Pruning residues · Soil nutrients · Indonesia · Home-field advantage

Abbreviations

C Carbon
CAF Complex agroforestry system

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R. R. Sari · D. M. A. Rozendaal · D. D. Saputra · M. van Noordwijk
Plant Production Systems Group, Wageningen University and Research, P.O. Box 430, 6700 AK Wageningen, The Netherlands

R. R. Sari (✉) · D. D. Saputra · K. Hairiah
Soil Science Department, Faculty of Agriculture, Brawijaya University, Malang 65145, Indonesia
e-mail: rika.sari@wur.nl; rr.sari@ub.ac.id

D. M. A. Rozendaal
Centre for Crop Systems Analysis, Wageningen University and Research, P.O. Box 430, Wageningen 6700 AK, The Netherlands

J. M. Roshetko · M. van Noordwijk
World Agroforestry, ICRAF Southeast Asia, 16001 Bogor, Indonesia

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CM	Cacao monoculture
CR	Crops
HFA	Home-field advantage
k	Decomposition rate/constant
L	Lignin
LUS	Land-use system
N	Nitrogen
Pp	Polyphenols
RF	Remnant forest
SAF	Simple agroforestry system
t_{50}	Half-life time

Introduction

Litterfall, along with root turnover, represents the primary biological pathway for element transfer from vegetation to the soil. The litter layer, formed by litterfall and consumed by comminutors and decomposers, constitutes the main resource of energy and matter for a diverse community of soil organisms connected by highly complex interactions (Bargali et al. 2015; Hättenschwiler et al. 2005). The interaction between litter and decomposers plays an important role in regulating nutrient and carbon cycling, maintaining soil fertility in forests and in agricultural systems (Karki et al. 2021a, b; Manral et al. 2020; Padalia et al. 2021; Yang et al. 2004). Standing litter protects the soil surface from runoff and erosion (Liu et al. 2017). In open-field agriculture based on annual crops, the litter layer usually is ephemeral, depending on the crops and soil tillage used, exposing the surface soil to radiation and splash-erosion. In forests with higher and more varied litter input, it is usually permanent but can be spatially heterogeneous, allowing an understorey vegetation to emerge.

Differences in litter dynamics can be explained by variation in litter quality, the total amount of litter input and seasonal patterns in litterfall combined with seasonal variation in biological activity. The conclusions regarding the relative importance of litter quality and environmental conditions on decomposition rates tend to depend on the type of variation (variables) included in the study (Aerts 1997; Bradford et al. 2016; Couteaux et al. 1995). A global study revealed that actual evapotranspiration (AET) was the strongest predictor of the litter decay rate (Aerts 1997), as it combines temperature and water availability as basis of biological activity. However, in the tropics, the role of litter chemistry still dominates. Litter decomposition rates in smallholder cacao agroforests in Ghana correlated with soil moisture content and pH, but not litter chemistry (Asigbaase et al. 2020). In contrast, litter quality was a predominant driver of decomposition rates along a land-use gradient, including cacao agroforestry at plot/farm scale (Dawoe et al. 2009; Fanin et al. 2016; Hoeber et al. 2020; Tanner 1981). In agroforestry landscapes with intermediate levels of tree cover between forests and open-field agriculture, the dynamics of the standing litter stock depend on tree density, species composition, phenology and management practices by the farmer (Hairiah et al. 2006). In annual cropping systems, in contrast, the litter layer is not permanent as a consequence of intensive management, which has been linked to a decline in soil fertility (Asase et al. 2008). Belowground carbon (C) stocks in annual cropping systems are around 40% lower than in forests (Hairiah et al. 2020), due to low root weight and low turnover in annual cropping systems (Saputra et al. 2020), and low C input into the soil through litter decomposition. In a mixed system such as cacao agroforestry, the litter layer consists of a mixture of leaves from cacao and various shade tree species. To guarantee provision of ecosystem services from the litter layer, enhanced understanding of variation in standing litter stocks throughout the year in different land-use systems is much-needed. In this study, we assess variation in litterfall and decomposition across a land-use gradient in a cacao agroforestry landscape in Indonesia.

Standing litter stocks represent the balance between the amount of litter reaching the soil surface per unit of time and the rate of decomposition. The amount of litterfall is influenced by tree species composition, stem density (Celentano et al. 2011), stand age (Köhler et al. 2008), soil fertility, and rainfall (Lopes et al. 2015; Souza et al. 2019). Fertile soil may result in optimum plant growth with higher aboveground biomass compared to unfertile soil. Higher basal area, tree density, and aboveground tree biomass usually increase litter production (Celentano et al. 2011; Schilling et al. 2016), whereas rainfall patterns generally determine the variation during the year (Lopes, 2015). The 'nature' of the litter, such as its physical characteristics (leaf thickness and size of the fragments), chemical and biological quality (cell and tissue structure) control the availability of food for decomposers (Gessner et al. 2010), but the biotic

and abiotic environment in which the decomposition occurs ('nurture') also affect the decomposition rate (van Noordwijk 1996). Chemical indicators of litter quality such as nitrogen content (N), C:N ratio, lignin (L), polyphenols content (Pp) or the ratios of L:N and (L+Pp):N can be used to predict decomposition rates (He et al. 2019; Mafongoya et al. 1997; Talbot and Treseder 2012). The C concentration indicates the energy available for microbial growth and activity (Smith 1994), but organic matter with high L content provides little or no energy to decomposers until the late stages of decomposition (Mafongoya et al. 1997), as lignin in cell walls physically protects cellulose and other cell wall constituents from degradation (Chesson et al. 1997). Polyphenolics (such as tannins) bind protein and as such slow down decomposition (Handayanto et al. 1997). Decomposition rates of litter mixtures generally do not equal the mean value of single species decomposition rates (Gartner and Cardon 2004; Steinwandter et al. 2019). A synergistic effect (faster decomposition in mixtures than expected) or an antagonistic effect (slower decomposition in mixtures than expected), thus non-additive effects, can occur (Liu et al. 2020). A synergistic effect occurs when in heterogeneous mixtures nutrients are transferred from high-quality to low-quality litter (Kuzyakov et al. 2000). High-quality litter provides accessible carbon compounds to support microbial growth (Hättenschwiler and Jørgensen 2010), which is beneficial for decomposing lower-quality litter. However, antagonistic effects occur when the presence of recalcitrant compounds (L and Pp) and proteins form resistant complexes (Hättenschwiler and Vitousek 2000) that inhibit microbial growth and activity (Schimel et al. 1998). A recent meta-analysis on the effects of species mixtures on litter decomposition revealed that these interactive effects between litter of different species depend on the context, and cannot be generalized (Porre et al. 2020).

Reciprocal litter exchange experiments tested the combined effect of litter quality and environmental conditions on the rate of litter dry weight loss in relation to soil conditions (biota, nutrient supply, temperature, soil moisture) in forests, agricultural fields and grasslands (Asigbaase et al. 2020; Hättenschwiler and Jørgensen 2010; Hoeber et al. 2020; Liu et al. 2010; Rachmawati et al. 2019; Schilling et al. 2016; Wang et al. 2015). Beyond effects of litter quality and microclimate, the interaction between substrate quality and composition of the microbial community also influences litter decomposition (Fanin et al. 2016; Fierer et al. 2005). If microbial communities decompose 'home' leaf litter faster than unfamiliar substrates, the net effect has been referred to as Home-Field Advantage (HFA) (Ayres et al. 2009; Veen et al. 2018), but negative interactions are also possible. In a recent study on HFA effects in shaded coffee systems, possible adaptation of microbial communities to the dominant food sources that determines the decomposition rate could not be distinguished from the effects of differences in microclimate between the land-use systems with and without shade trees (Schmitt and Perfecto 2021). Important uncertainties thus remain regarding the magnitude and direction of such interactions (Freschet et al. 2012), particularly for forest-agriculture mosaics in the tropics.

Specific questions on the dual role (soil protection and nutrient supply) of the litter layer in agroforestry systems in the humid tropics, with soil protection required from high rainfall intensities, exist for cacao production systems. As the leading cacao producer outside of West Africa, Indonesian smallholders produce cacao mostly on the island of Sulawesi. Cacao is grown in monocultures and intercropped with various shade tree species such as fruit trees, timber, and multipurpose tree species (MPTS) like *Gliricidia sepium* in simple and complex agroforestry systems. Complex agroforestry systems usually have a closed, multi-strata canopy compared to cacao monocultures. Complex cacao agroforests improve the structure of degraded soils resulting from forest to agriculture conversion (Saputra et al. 2020), and increase the soil water buffering capacity, which enhances the drought tolerance of the system (Gusli et al. 2020). Shade trees in agroforestry systems can also improve soil fertility (Wartenberg et al. 2019). However, knowledge on how to balance the litterfall and its decomposition rate to maintain soil surface cover and nutrient supply to the soil is lacking. The quantity and quality of organic matter input (litterfall, roots) in cacao ecosystems are expected to vary due to floristic and structural differences. Therefore, microclimate variation could jointly affect soil organism activity that influences the decomposition rate and determines standing litter stocks across the land-use gradient. Pruning in cacao-based agroforestry systems is essential to optimize cacao production, to allow sufficient light for cacao, and to decrease humidity to prevent the spread

of pests and diseases (Norgrove and Hauser 2013). Pruning residues in cacao agroforests are an essential input of organic matter (with values up to 4 Mg ha^{-1} $year^{-1}$) (Fassbender et al. 1991; Schneidewind et al. 2018) that contribute to sustaining soil nutrient availability (Schroth et al. 2001; van Vliet et al. 2015), such as N in particular. Generally, the pruning residues of cacao and shade trees (frequently *Gliricidia*) are left as litter on the soil surface to remain in the system. This addition may modify litter decomposition rates and influence soil C and N change. Understanding litter (including pruning residues) residence time and its contribution to soil nutrient addition is important to maintain a permanent litter layer, and to ensure continuous organic matter input.

In this study, we evaluated variation in litterfall quality and quantity, and unravel the effect of litter quality, microclimate and HFA on decomposition rates, and their relative importance, across a land-use gradient in a cacao agroforestry landscape. By combining results, we assessed how litterfall and decomposition influence standing litter stocks over time in cacao-based agroforestry systems compared to a cacao monoculture, annual crops, and remnant forest. We addressed the following research questions: (1) How does litterfall vary across land-use systems, and during the year?; (2) How do litter quality, microclimate, and HFA influence litter decomposition rates across the land-use gradient?; (3) Does the litter decomposition rate determine the relative change of soil organic C and N across the land-use gradient?; and (4) Do the mixed pruning residues of cacao and *Gliricidia*, or *Fagraea fragrans* (a local forest tree species), modify the decomposition rate, net N loss in the residues, and the change of soil C and N in cacao agroforestry compared to a cacao monoculture?

We expected to find that litterfall is seasonal and higher in remnant forest than in cacao production systems, particularly during the drier months. We hypothesized that variation in both litter quality and microclimate across land-use systems will be equally important drivers of litter decomposition rates. We expected that faster decomposition will result in a higher change of soil C and N, with stronger changes in open systems than in cacao-based agroforestry systems and remnant forest. We expected that mixed pruning residues of cacao with *Gliricidia*, or with *Fagraea fragrans*, will have a faster decomposition rate than leaves from a single species (cacao, *Gliricidia*, or *Fagraea fragrans* alone), with higher net N loss and soil C and N change, particularly in cacao agroforestry systems.

Materials and methods

Overview

To answer the research questions, we monitored litterfall across a land-use gradient ranging from annual crops to cacao production systems, to remnant forests, in Southeast Sulawesi, Indonesia. We performed two litter decomposition experiments. A reciprocal litter transfer experiment was conducted to assess the influence of litter quality, microclimate, and HFA on decomposition rates. A decomposition experiment based on different combinations of pruning residues (cacao, *Gliricidia* as a nitrogen fixing species, *Fagraea fragrans*) was conducted to assess the effect of pruning residues on decomposition rates to improve management strategies for cacao agroforestry systems. We included pruning residues from the local tree species *Fagraea fragrans* since it is frequently included in cacao-based agroforestry systems as a shade tree. These combinations were selected to represent litter in the complex and simple agroforestry systems. Litter combinations were tested in equal proportions to test for interactions in decomposition rates. Finally, we estimated the standing litter stock over the year from the litterfall and the decomposition rate.

Study site

We conducted our study in the Konawe District, Southeast Sulawesi, Indonesia (3◦15'0" –5◦13'0" S and 121◦22'30" –122◦31'0" E) across a land-use gradient. Cacao is the most prevalent cash crop in the region and planted in monocultures and diversified agroforestry systems. Most of the cacao is planted together with *Gliricidia sepium*, fruit trees (*Durio zibethinus, Lansium domesticum, Nephelium lappaceum*, and *Mangifera indica*), and timber trees (*Tectona grandis*) as shade trees that provide products to address the daily needs of farmers and to increase farmer income. Farmers prune shade trees and cacao during the rainy season (around June) at least once a year. Soil and fertilizer management varies from none

to insufficient fertilizer application (Hoffmann et al. 2020; Wartenberg et al. 2019). The annual rainfall recorded is generally 1500–1900 mm (BPS 2015), and the temperature varies from 24 to 31 °C. Soil texture ranges from silt loam to silty clay loam across the land-use gradient (Saputra et al. 2020).

We established a total of fifteen 20 m x 20 m permanent plots (Sari et al. 2020), across five LUS: (1) remnant forest (RF); (2) complex cacao agroforestry (CAF), the combination of cacao with fruit trees, timber, and the nitrogen-fixing shade tree *Gliricidia sepium*; (3) simple cacao agroforestry (SAF), cacao with mainly *Gliricidia sepium* as shade tree; (4) monoculture cacao (CM); and (5) annual crops (CR). The criteria for plot selection were a minimum cacao age of 9 years, a slope ranging from 0 to 15%, and similar soil texture (see Sari et al. (2020) for more details).

Annual litterfall production

Litterfall was measured during a one-year period (June 2015 – May 2016) using litter traps. Two traps of 1.5 m x 3 m, with a 1 mm-mesh size (Hairiah et al. 2006) were placed below the canopy of each plot, and installed 80 cm above the ground (Mohan Kumar 2007) to prevent animal disturbance. We collected the litter every week and sorted the litter into leaves, branches, fruits, and flowers. Dry weight was determined by oven-drying the litter samples for 48 h at 60^0 C (Negash and Kanninen 2013). To assess litter quality, composite dried litter samples per plot were used. For each sample, N content, lignin content, and polyphenols content were determined. For N content, the Kjeldahl method was used (Gallaher et al. 1976). Lignin and polyphenols content were determined following the method of Goering and Van Soest (1970); and Ingram and Anderson (1993), respectively.

Experimental design

The decomposition experiments were performed in June – October 2016. The first decomposition experiment was conducted to assess how litter quality and microclimate influence decomposition rates, and how these influence soil C and N content. A reciprocal litter transfer experiment was conducted by comparing decomposition rates of litter collected in four LUS (RF, CAF, SAF, CM) across a gradient of environmental conditions in five LUS (RF, CAF, SAF, CM, and CR). Litter from all origins was placed in the original and each of the other land-use systems, with three replicates per land-use system. An average of 77 g air-dried litter (equivalent to the amount of standing litter observed in the LUS; Table 1) was put in the litter bags with a size of 25 cm x 30 cm and a mesh size of 2 mm (Ingram and Anderson 1993). A total of 300 litter bags (five LUS, four types of litter, three replicates, five observations in time) were placed across the land-use systems. They were pinned to the soil surface to avoid litter loss due to litter bag movement. We measured the remaining litter mass at 1, 2, 4, 8, and 16 weeks after the start of the experiment, based on 36 litter bags for each point in time. The remaining litter was cleaned of adhering soil by floating it in a bucket with water. The floating litter was drained in a filter, and oven-dried at 60^0 C for 48 h. The litter dry weight was corrected by its ash content by heating the sub-samples in a muffle

Table 1 Characteristics of the study sites: the cacao production systems and the remnant forest (modified from Sari et al. (2020))

Land-use systems	Tree density, trees ha^{-1}	Total basal area, m^2 ha^{-1}	Number of species	Dominant species	Litter, Mg ha^{-1}
Remnant forest (RF)	1,275±151	18.42±2.61	28	*Metrosideros petiolata, Homalium foetidum*	6.98±2.24
Cacao-based complex agroforestry (CAF)	1,317±82	9.14±0.24	18	*Theobroma cacao, Durio zibethinus, Lansium domesticum*	7.02±1.67
Cacao-based simple agroforestry (SAF)	1,267±219	7.63±0.22	4	*Theobroma cacao, Gliricidia sepium*	5.51±1.26
Cacao monoculture (CM)	900±29	8.32±1.31	2	*Theobroma cacao*	4.26±0.22

Average values (± standard error (SE) for a total of 15 plots are indicated)

furnace at 400-500^0 C for 4 h. The N content (Kjeldahl method; Gallaher et al. (1976)) was determined for each litter sample at 1, 4, and 16 weeks after the start of the experiment.

In the second decomposition experiment, we assessed the effect of the addition of pruning residues from different tree species on decomposition rates and net N loss. We compared five treatments, using pruning residues of: (1) cacao alone, (2) cacao and *Gliricidia sepium (Fabaceae)*, (3) *Gliricidia* alone, (4) cacao and a local forest tree species (*Fagraea fragrans*, local name: Kolahi), and (5) *Fagraea fragans* alone. Leaf material was collected outside the permanent plots at the same time as farmers' prune. The amount of pruning residues in litter bags was equal to the average annual litter production in all LUS (approximately 4 Mg dry mass ha^{-1}), with a 1:1 mass ratio for the mixture treatments. We followed the same methods as in the first experiment. A total of 150 litter bags (two LUS, five litter sources, three replicates, and five observations in time) were placed in CAF and CM. We measured the remaining litter mass at 1, 2, 4, 8, and 16 weeks after the start of the experiment, and we determined N content of the litter samples at 1, 4, and 16 weeks.

For both experiments, soil samples were collected under the litter bags from 0 to 10 cm depth, at the time of litter bag collection, at 1, 4, and 16 weeks after the start of the experiment. The total C (Walkley and Black 1934) and N content (Kjeldahl method; Gallaher et al. (1976)) were determined for each soil sample. Standing litter samples were collected at ten points within each plot using a 0.5 × 0.5 m frame. Litter samples were oven-dried for 48 h at 60 °C.

Rainfall and microclimate

Rainfall was recorded weekly, and every time after a rain event, using two plastic cylinders installed in an open field near the research plots during a year (June 2015 to May 2016). Air and soil temperature were measured weekly at three different points close to the litterbags in each permanent plot between 6 and 8 am, using a mercury thermometer from June 2015 to October 2016. Soil temperature was recorded weekly at three different points near the litterbags in each plot at soil depths of 0-10 cm, 10-20 cm, and 20-30 cm. Volumetric soil moisture content (ThetaProbe^{TM}, Delta-T Devices) was measured at four different points in the topsoil (0-10 cm) in each plot at the start of the experiment.

Estimating decomposition rates

To compare the decomposition rates across the land-use gradient at the same temperature, we estimated the decomposition rate using a temperature-corrected exponential decay function, modified from Olson (1963):

$$\frac{X_t}{X_0} = e^{-kI_t t} \tag{1}$$

where, X_t is proportion of initial mass remaining at time t (in g), X_0 is proportion of initial mass (in g), k is decomposition rate (k; week^{-1}), t is time (in weeks), and I_t is an index of temperature effects based on the average over the n weeks of the measurement period. I_t was calculated as the product of daily values, as:

$$I_t = \left(\Pi_1^n Q_{10}^{(T-T_{ref})/10} \right)^{1/n} \tag{2}$$

where, Q_{10} is the temperature response rate of biological processes, T is temperature (in ^{o}C), and T_{ref} is a reference temperature of 20^{o}C. We used a Q_{10} of 2.2, which is considered an appropriate estimate of Q_{10} for agricultural soils (Delogu et al. 2017). The half-life time (t_{50}) was calculated based on the k value as follows (Hairiah et al. 2006; Olson 1963):

$$t_{50} = -\ln(0.5)/k \tag{3}$$

where t_{50} is the litter half-life time (in weeks).

The mean HFA was calculated to obtain the percent increase in decomposition rates in the 'home' environment compared to the same litter source when tested in an 'away' environment, as follows (Austin et al. (2014):

$$Mean\ HFA = \frac{(k_{home} - k_{guest})}{k_{guest}} \times 100 \tag{4}$$

where k_{home} is the decomposition constant in the home/original environment, and k_{guest} is the average decomposition constant across all away environments. If the mean HFA is equal to zero, then the average rate of decomposition does not differ between the home site and the reciprocal sites; if HFA is larger than zero, then the average rate of decay is higher at

home than at the reciprocal site; and if HFA is less than zero, then the average rate of decomposition is higher at reciprocal site than at home. Such effects can be due to differences in micro-climate, soil fertility (e.g. availability of nitrogen for immobilization), or the degree to which the decomposer community is adapted to the litter source. Microclimate effects were in part represented by the temperature index.

The relative change of net N loss from the litter was expressed by the change of N content at each time of observation relative to the initial content. For instance, the relative net N loss at week 4 was calculated from the change of N content of certain litter type between week 1 and 4 relative to week 0 (initial content). We calculated the relative change in soil C and N in the same way.

To explore the variation in standing litter stocks over time, we adapted a simple spreadsheet model developed by van Noordwijk (2020). The amount of standing litter over a year was predicted based on the litterfall and the decomposition rate (litter half-life time, t_{50}) after the experiment was performed. The amount of standing litter at time t relative to annual litterfall was derived as integral over the litterfall rate and the time elapsed. The seasonal litterfall pattern was approximated by a combination of sinus functions, characterized by a peak week and a power parameter that determines the shape of the curve. Before using the output of the model, we assessed whether the predicted standing litter value generated by the model after a year agreed with the observed standing litter stock at the beginning of the experiment.

Statistical analysis

We used two-way ANOVAs, followed by Tukey's HSD (honestly significant difference) post-hoc tests, to assess (1) whether the litter production differed between the dry and wet season across the land-use gradient, (2) whether the decomposition rate varied among land-use systems and litter origin in both experiments, (3) whether the relative change of soil C and N content differed among litter origins across the land-use systems, and (4) whether the net N loss varied among the different pruning residues in CAF compared to CM. We tried all the combination of two-way interactions and only included them in the analysis when it improved the model fit based on the Aikaike Information Criterion (AIC) value. The statistical significance threshold was set at $\alpha = 0.05$. The relative soil C change in the second experiment was square root transformed prior to analysis to meet the normality assumption. We performed linear regressions to assess whether net N loss from the pruning residues was associated with an increase in soil C and N levels. We are aware that observations over time within a single plot may not be independent, and therefore we analysed our data also with linear mixed-effects models by including plot as random effect, and land-use system and litter origin as fixed effects. However, since the random effect did not explain any of the variation in the litter decomposition rates, net N loss, and the relative change of soil C and N in both experiments, we chose to use analysis of variance. We tested the differences in (1) microclimate parameters (air temperature, soil temperature and moisture) across a land-use gradient, (2) chemical leave characteristics (for litterfall and pruning residues) among litter origins, and (3) standing litter among land-use gradient using one-way ANOVAs, followed by Tukey's HSD post-hoc tests.

To assess how litter quality, microclimate and HFA influence the decomposition rate within cacao production systems, and their relative importance, we fitted a multiple regression model. We included total N, (L+Pp):N ratio, HFA, soil temperature, and soil moisture as explanatory variables. We excluded lignin, polyphenolics, and air temperature from the analysis, as they were strongly correlated (Pearson's $r > 0.75$) to the total N, (L+Pp):N ratio, and soil temperature, respectively. We standardized all explanatory variables before analysis by subtracting the mean and dividing by the standard deviation, to be able to compare effect sizes (Andrews 1974; Gelman and Hill 2006). All statistical analyses were performed in R 4.0.0 (R-Core-Team 2020).

Results

Litterfall and standing litter stocks across the land-use gradient

Monthly litterfall differed significantly across land-use systems, and between the dry and wet season. The highest average monthly litterfall was found in RF (0.62 Mg ha^{-1} month^{-1}), while in CAF, SAF,

and CM, litterfall ranged from 0.42 to 0.52 Mg litter ha^{-1} $month^{-1}$. Overall, litterfall was marginally higher in the dry season (on average 0.58 Mg ha^{-1} $month^{-1}$) than in the wet season (0.42 Mg ha^{-1} $month^{-1}$) (Fig. 1b). Monthly litterfall in RF increased by as much as 65% in October and reached a peak in November (1.8 Mg ha^{-1} $month^{-1}$), the driest month of the year (Fig. 1a). In cacao production systems, the peak was in July, however, there was a significant increase in litterfall during dry months. The peak of litterfall in cacao systems appeared after one month of dry conditions, while in remnant forest the peak was reached after two months, suggesting that cacao production systems had lower buffer capacity compared to RF. We found that litterfall increased with the total tree basal area per ha (Pearson's r=0.84, P<0.001). The composition of litterfall differed between the cacao-based agroforestry systems, RF, and CR. Almost 80% of the litterfall in CAF, SAF and CM consisted of leaves. Shade trees contributed nearly 30% of all leaf material in the litter layer in CAF and SAF. Litterfall in RF consisted of 56% leaves, 41% woody parts, and the rest consisted of flowers and fruits. Standing litter stocks in RF were higher compared to CAF, SAF, and CM (Fig. 1c).

Litter quality

Litter quality differed across land-use systems due to differences in tree species composition. Across all land-use systems, litter quality was generally low, as litter had a high L (>15%), Pp (>3%) content, and (L+Pp):N ratio (>10). L and Pp content differed significantly among litter from different origins. L and Pp content was highest in CAF litter followed by RF litter. In contrast, the SAF litter had the lowest percentage of L, Pp, and (L+Pp):N ratio compared to the litter from the other land-use systems (Table 2), as leaf litter from SAF consisted of cacao and *Gliricidia* leaves.

Variation in microclimate across the land-use gradient

Air and soil temperature and soil moisture were significantly different across land-use systems. RF had a relatively cool microclimate, while in CR temperatures were the highest. Cacao agroforestry and monoculture had intermediate air and soil temperature levels (Fig. 2a and b). Within cacao production systems, CAF had the lowest air and soil temperature, with no significant difference between SAF and CM. Soil moisture was significantly higher in SAF (16.3%), followed by CAF, CM and CR (14, 13.6, and 12.2%, respectively), while RF had the lowest soil moisture (8.4%; Fig. 2c).

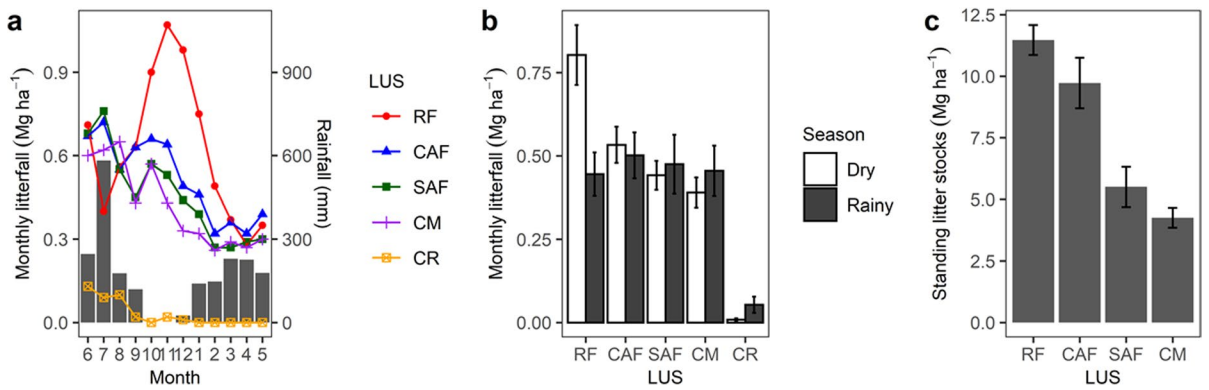


Fig. 1 Litterfall in different land-use systems across a land-use gradient in Southeast Sulawesi, Indonesia: **a**) Litterfall and rainfall per month, **b**) Seasonal litter production during June 2015 – May 2016, and **c**) Standing litter stocks in the land-use systems in June 2016 (means ± SE)) (LUS=land-use system; RF=remnant forest; CAF=cacao-based complex agroforestry; SAF=cacao-based simple agroforestry; CM=cacao monoculture; CR=annual crops)

Table 2 Chemical characteristics of (a) litterfall, and (b) pruning residues from various land-use systems (RF=remnant forest; CAF=cacao-based complex agroforestry; SAF= cacao-based simple agroforestry; CM=cacao monoculture; F= *Fagraea fragrans* alone; F+Cc= *Fagraea fragrans*+cacao; Cc=cacao alone; Cc+G=cacao+*Gliricidia* leaves; G=*Gliricidia* alone)

Litter source from	Nitrogen (N), %	Lignin (L), %	Polyphenols (Pp), %	(L+Pp):N
a) Litter transfer experiment				
RF	1.14 ± 0.01^{bc}	22.93 ± 0.04^{b}	6.30 ± 0.03^{b}	25.79 ± 0.13^{b}
CAF	1.13 ± 0.02^{c}	28.57 ± 0.04^{a}	9.37 ± 0.04^{a}	32.81 ± 0.40^{a}
SAF	1.19 ± 0.01^{ab}	19.28 ± 0.01^{d}	2.74 ± 0.02^{d}	18.25 ± 0.13^{c}
CM	1.22 ± 0.01^{a}	20.07 ± 0.02^{c}	3.37 ± 0.04^{c}	18.94 ± 0.08^{c}
b) Pruning residues decomposition experiment				
F	2.13 ± 0.07^{a}	26.50 ± 0.12^{b}	7.53 ± 0.07^{e}	16.16 ± 0.60^{a}
F+Cc	2.38 ± 0.06^{a}	28.43 ± 0.18^{a}	7.03 ± 0.06^{a}	16.16 ± 0.47^{a}
Cc	2.32 ± 0.18^{ab}	25.74 ± 0.29^{b}	4.53 ± 0.11^{b}	13.16 ± 0.87^{b}
Cc+G	2.88 ± 0.11^{bc}	24.18 ± 0.08^{c}	3.21 ± 0.07^{c}	9.66 ± 0.33^{c}
G	2.99 ± 0.21^{c}	21.27 ± 0.16^{d}	2.78 ± 0.07^{d}	8.33 ± 0.80^{c}

Three plots were included per land-use system

Note: the values displayed are means ± SE.; different letters within a variable are significantly different at $P < 0.05$

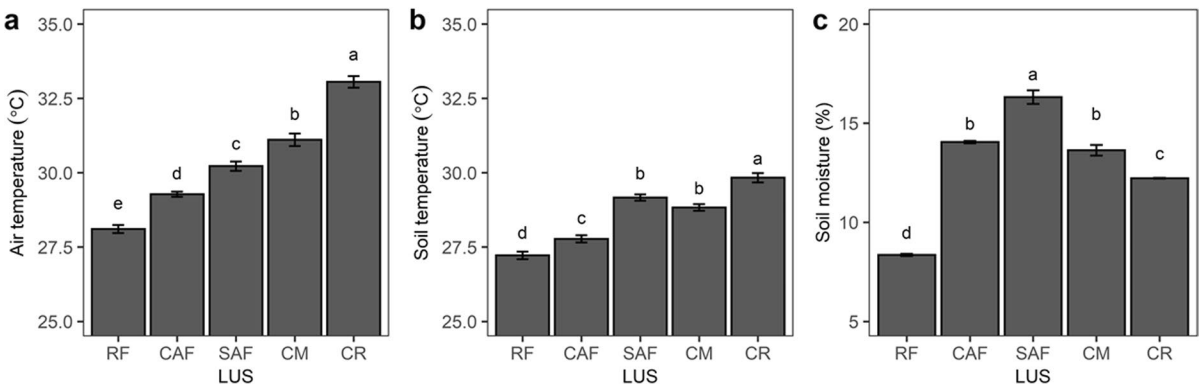


Fig. 2 Microclimate parameters across a land-use gradient in Southeast Sulawesi, Indonesia: (**a**) Air temperature, (**b**) Soil temperature, and (**c**) Soil moisture (means ± SE). (LUS=land use system; RF=remnant forest; CAF=cacao-based complex agroforestry; SAF= cacao-based simple agroforestry; CM=cacao monoculture; CR=annual crops)

Decomposition rates of litter from different origins across the land-use gradient

The decomposition rate varied for litter that originated from the different land-use systems (Table 3). Litter from SAF had the highest decomposition rate, followed by litter of CM and CAF, while the decomposition rate of litter from RF was the lowest. The relatively low-quality litter from CAF consisted not only of cacao leaves, but also (35% of the total) of leaves from slow-growing shade tree species such as *Lansium domesticum, Nephelium lapaceum, Magnifera indica, Tectona grandis*, and some remnant forest tree species (*Fagraea fragrans* and *Albizia procera*). Litter decomposition rates did not significantly differ among land-use systems. We found a positive mean HFA effect (8.68) in SAF, where the decomposition rate was higher in the original/home environment than in the other land-use systems. However, we did not find a HFA effect in RF (-52.54), CAF (-0.83) and CM (-19.15).

We assessed the relative importance of inherent litter quality and microclimate on decomposition rates, using multiple linear regression. Across the land-use

Table 3 Decomposition rates (at a reference temperature of 20°C) of litter originating from different land-use systems across a land-use gradient in a litter-transfer experiment (LUS=land-use system; RF=remnant forest; CAF=complex agroforestry system; SAF=simple agroforestry; CM=cacao monoculture)

LUS	Litter origin	k, week^{-1}	R^2	Mean residence time ($1/k$), week	Half-life time t_{50}, week
Remnant forest	RF	0.007	0.887	140	97
	CAF	0.011	0.849	93	65
	SAF	0.023	0.759	43	30
	CM	0.021	0.904	49	34
Complex agroforestry	RF	0.009	0.856	108	75
	CAF	0.010	0.975	103	71
	SAF	0.020	0.922	49	34
	CM	0.017	0.902	60	41
Simple agroforestry	RF	0.016	0.725	64	45
	CAF	0.010	0.903	105	73
	SAF	0.023	0.836	44	31
	CM	0.020	0.748	50	35
Cacao monoculture	RF	0.021	0.641	48	33
	CAF	0.015	0.843	68	47
	SAF	0.023	0.855	43	30
	CM	0.016	0.868	64	44
Crops	RF	0.014	0.821	71	50
	CAF	0.014	0.803	71	50
	SAF	0.021	0.928	48	34
	CM	0.022	0.786	45	31
Means		*0.017*		*68*	*47*
SE		*0.001*		*6.15*	*4.15*

gradient, decomposition rates were strongly driven by a significant, negative effect of (L+Pp):N (Fig. 3a, b). Soil moisture, HFA, and soil temperature did not have a significant effect (Fig. 3a).

Changes in soil C and soil N content in response to decomposition across a land-use gradient

To assess whether the decomposition rates affect soil

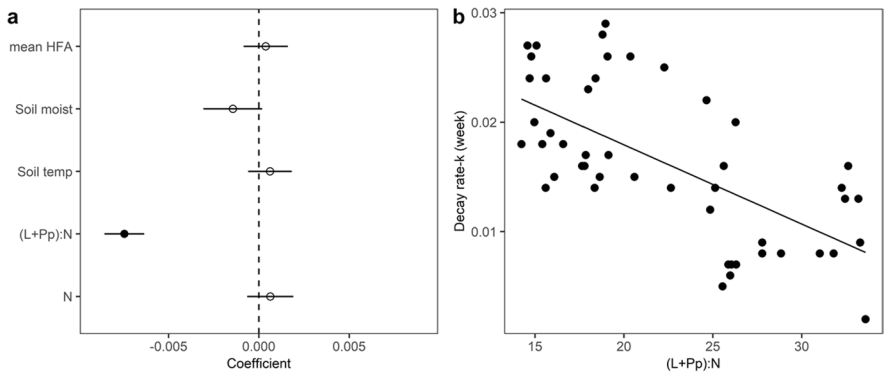


Fig. 3 **a**) The effect of litter quality, microclimate, and mean HFA on the rate of litter decomposition (k) at a reference temperature of 20°C. Standardized coefficients with 95% confidence intervals are indicated for all explanatory variables. A negative coefficient indicates a negative relation, while a positive coefficient indicates a positive relation. Filled symbols represents a significant response, while open symbols represent an insignificant response. **b**) Relationship between (L+Pp):N and the decomposition rate (the other explanatory variables were kept constant at the mean)

C and N content, we evaluated the relative change of soil organic C and N directly below the litterbags across the land-use gradient over time. We included the interaction of land-use and time of observation in the model for this analysis because it significantly improved model fit. We found a significant effect of land-use systems and week of observation on the relative change in soil C. The highest change in soil C was found in SAF at week 16. Whereas, we found little change of soil C in CM, particularly at week 1. Overall, soil C content directly below the litter bags increased on average 38% (ranged from 1 to 69%) after 16 weeks for all litter origins in all land-use systems. Generally, the relative soil C change increased over time (except for RF; Fig. 4a), with the strongest increase in week 16 (a 16.5% increase). Only in RF, the relative change in soil C generally decreased over time for litter of all origins. The decomposition rate (*k* value) and the relative change in soil C content were not significantly correlated.

The relative change in soil N content differed significantly among litter from different origins, and over time. For this analysis, we included the interaction between land-use system and time since it significantly improved model fit. The relative change of soil N in SAF and CM at week 16 was the highest, while RF at week 1 and CAF at week 4 were the lowest. Most of the litter origins in all land-use systems decreased approximately 7% in the first week of the experiment relative to the start of the experiment, and gradually increased until week 16 (Fig. 4b). However, the soil N content directly below the litter bags increased approximately 2% (with a range from -9 to 16%) compared to the initial content after week 16 in all land-use systems. We also found no correlation between decomposition rate and the relative change of soil N. However, we unexpectedly found that both relative soil C and N content under SAF litter in SAF had the highest change compared to litter from the other origins that was placed in the home environment.

Net N loss from pruning residues during the decomposition process

To assess the role of pruning residues in modifying the decomposition rate, net N loss and soil C and N change, we evaluated different combinations of single vs. mixed species pruning residues. The decomposition rate was significantly different among pruning residues and across the land-use systems. *Gliricidia* had the fastest decomposition compared to cacao and

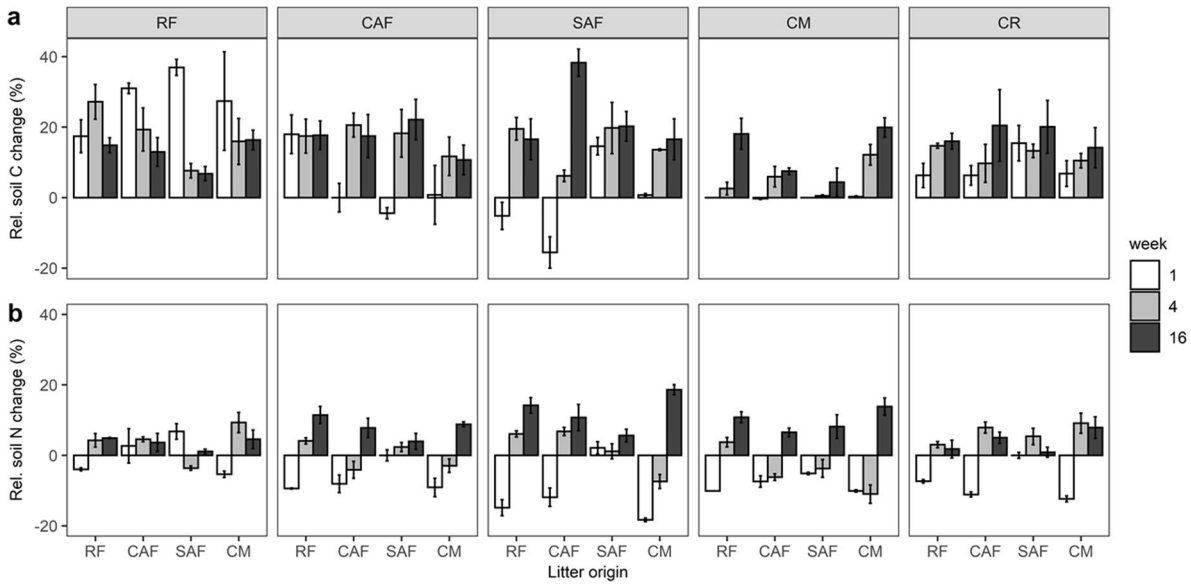


Fig. 4 The relative change in **a**) soil C and **b**) N underneath litterbags with litter from various origins during sixteen weeks across the land-use gradient (means ± SE). (RF=remnant forest; CAF=cacao-based complex agroforestry; SAF=cacao-based simple agroforestry; CM=cacao monoculture; CR=crops)

Fagraea fragrans alone, while the combination of cacao and *Gliricidia* decomposed faster than the combination of cacao and *Fagraea* (Table 4). Combining relatively fast and slow decomposing leaves increased or decreased the decomposition rate by 1 to 30% compared to pruning residues from a single species. The decomposition rate of the mixture of cacao and *Gliricidia* leaves (0.027 week^{-1}) was lower than the mean decomposition rate (0.036 week^{-1}) of cacao and *Gliricidia* alone. However, when comparing decomposition rates of mixtures to single-species litter, the mixture of cacao and *Gliricidia* decomposed significantly faster (twice as fast) than cacao leaves alone, but 50% slower than *Gliricidia* alone. For the mixture of cacao and *Fagraea fragrans*, the decomposition rate (0.016 week^{-1}) was slightly higher than the average (0.015 week^{-1}) of cacao alone and *Fagraea fragrans* alone. The mixture of cacao and *Fagraea fragrans* decomposed 35% faster than cacao alone, but 10% slower than *Fagraea fragrans* leaves alone.

The amount of net N loss did not significantly differ among the type of pruning residues and land-use systems. However, the amount of net N loss tended to be higher from the pruning residues that included *Gliricidia* than for the other treatments, as *Gliricidia* had a higher N content that increased decomposition rates (Fig. 5). Overall, 27% (range: 14 to 41%) of litter N content was lost after 16 weeks for most pruning residues in all land-use systems.

We found a significant effect of land-use system on the relative change in soil C over time. Overall, the total soil C change in CAF after 16 weeks of observation was marginally higher than in CM (Fig. 6a). There was no significant difference in the change of

Table 4 Decomposition rates (at a reference temperature of 20°C) of various combinations of pruning residues in CAF and CM (LUS=land-use system; CAF=complex agroforestry system; CM=cacao monoculture; F= *Fagraea fragrans* leaves alone; F+Cc= *Fagraea fragrans* +cacao; Cc=cacao alone; Cc+G=cacao+*Gliricidia* leaves; G=*Gliricidia* alone)

LUS	Litter treatment	*k*, week^{-1}	R^2	Mean residence time (1/*k*), week	Half-life time t_{50}, week
Complex agroforestry	F	0.014	0.95	70	49
	F + Cc	0.013	0.95	75	52
	Cc	0.011	0.97	94	65
	Cc + G	0.024	0.87	42	29
	G	0.043	0.45	23	16
Cacao monoculture	F	0.022	0.97	45	30
	F + Cc	0.019	0.91	52	36
	Cc	0.013	0.96	76	52
	Cc + G	0.031	0.83	32	22
	G	0.078	0.79	13	9
Means		*0.027*		*52*	*36*
SE		*0.006*		*8.20*	*5.69*

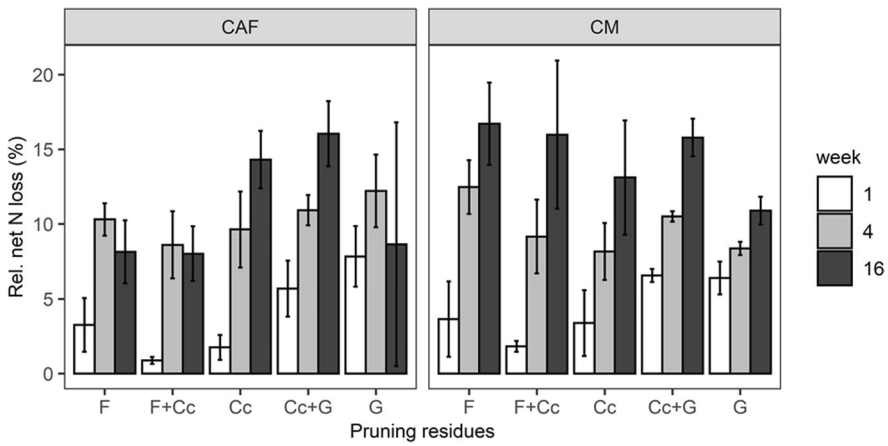


Fig. 5 The relative change in net N loss in different types of pruning residues during the decomposition process (means ± SE) (CAF=cacao-based complex agroforestry; CM=cacao monoculture F=*Fagraea fragrans* leaf; F+Cc=*Fagraea fragrans* + cacao; Cc= cacao, Cc+G=cacao + *Gliricidia*, G=*Gliricidia*)

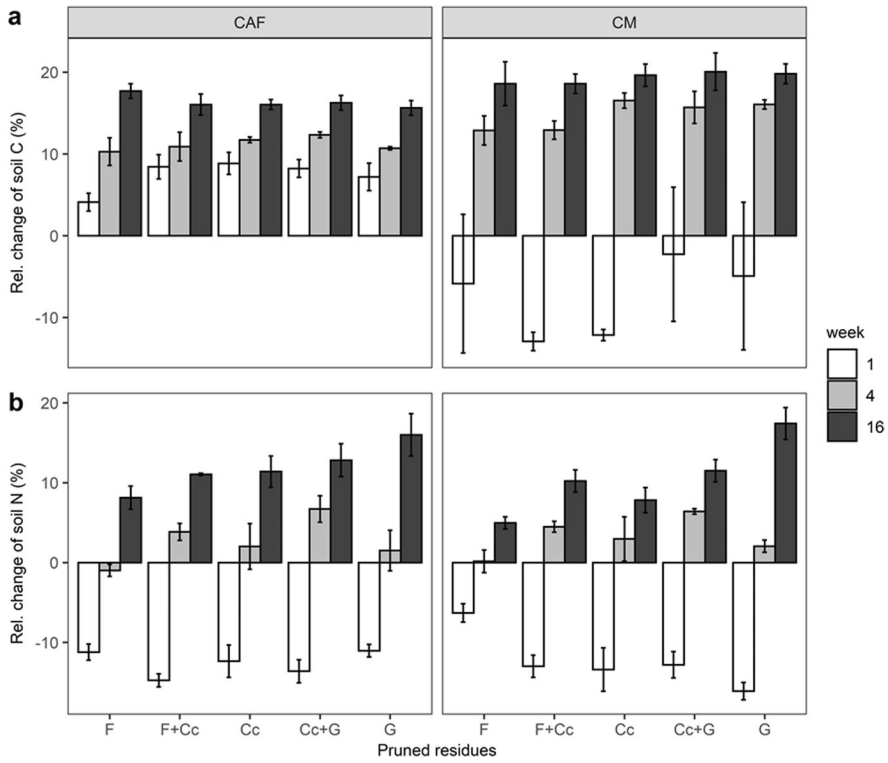


Fig. 6 Relative change in **a**) soil C and **b**) N content underneath types of pruning residues during the decomposition process (means ± SE). (CAF=cacao-based complex agroforestry; CM=cacao monoculture F=*Fagraea fragrans*; F+Cc=*Fagraea fragrans* + cacao; Cc= cacao, Cc+G=cacao + *Gliricidia*, G=*Gliricidia*)

soil N between land-use systems, but we found a significant effect regarding the type of pruning residues on the relative change of soil N content over time. As expected, the addition of soil N was highest for *Gliricidia* leaves alone (Fig. 6b). The relative change in soil N was positively correlated to the decomposition rate (Pearson's r=0.46 and P=0.01), but was more strongly, negative correlated to (L+Pp):N (Pearson's r=-0.71 and P<0.01). Additionally, the relative change in soil N, significantly increased with the amount of net N loss from the pruning residues across all treatments (Online Resource 2), whereas the relative change of soil C was not related to the decomposition rate and (L+Pp):N.

Temporal variation in standing litter stocks

We found that standing litter stocks across the land-use gradient were significantly related to litterfall and the decomposition rate (Online Resource 3). Standing litter stocks increased with increasing litterfall and decreased with increasing decomposition rates. We estimated the temporal variation in litter stocks based on litterfall and the decomposition rate (litter half-life time, t_{50}). Predicted standing litter stocks by the model after a year agreed well with the observed standing litter stock at the start of the experiment (R^2=0.91, P≤0.001, Fig. 7b). The intra-annual variation in standing litter in cacao production systems was low compared to RF (Fig. 7a). The temporal variation in the standing litter stock was identical over the year for all cacao production systems, with the lowest, estimated standing litter stocks during the rainy season (week 37 – 52 and week 1-12) and a gradual increase at the beginning of the dry season. A similar pattern was found in RF, but with a stronger fluctuation in standing litter stocks over the year. The standing litter in RF was predicted to first decline, with a 30% lower standing litter stock at the end of the rainy season (week 20), before a strong increase during the dry season due to high litter input.

Discussion

Seasonal variation in litterfall

We investigated the variation in litterfall across a land-use gradient. The annual litter production in

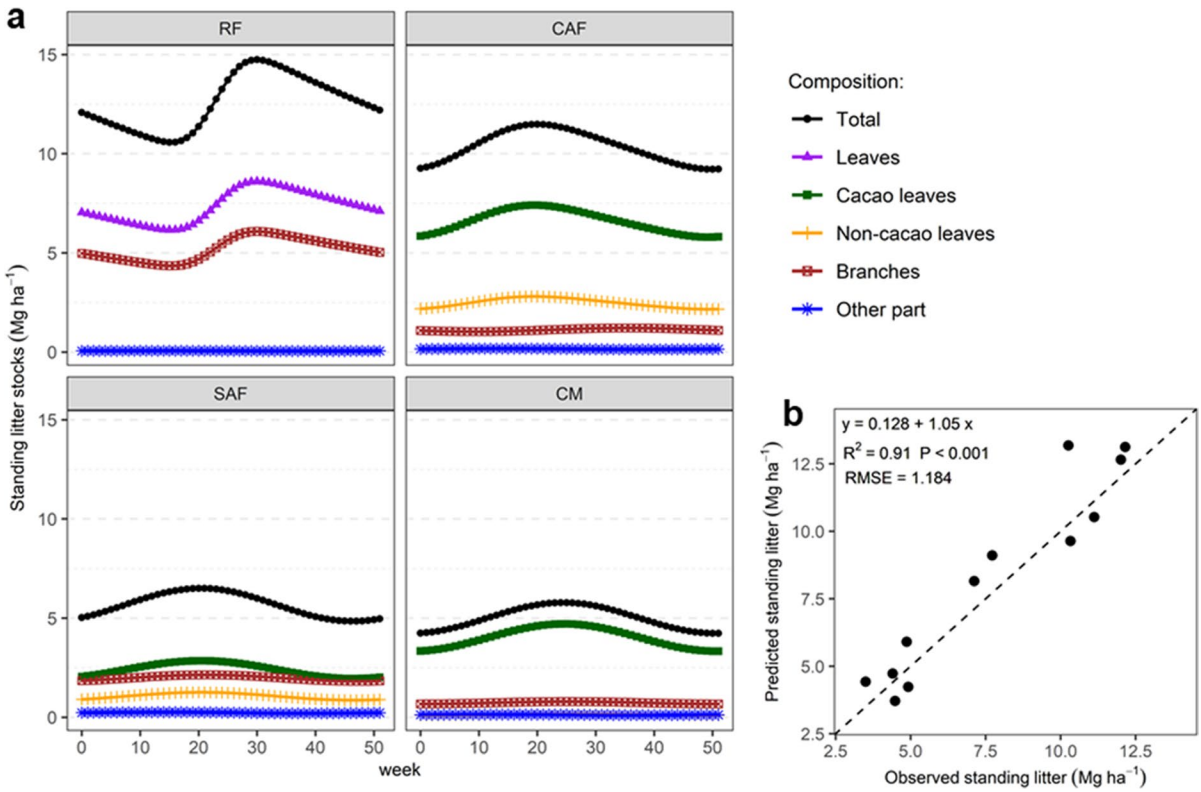


Fig. 7 **a**) Estimated standing litter stocks during the year based on litterfall production and decomposition rates in cacao production systems and remnant forest, **b**) Observed versus predicted standing litter stocks across all land-use systems (RF=remnant forest; CAF=cacao-based complex agroforestry; SAF= cacao-based simple agroforestry; CM=cacao monoculture)

CAF was the highest compared to SAF and CM, but not as high as RF. CAF had the highest tree density among all cacao production systems, with older forest remnant trees as shade trees, such as *Albizia procera* and *Fagraea fragrans*, which likely increased litterfall (Sari et al. 2020). Tree density, diversity, forest age and canopy cover influence the amount of litterfall in tropical forest (Celentano et al. 2011; Chave et al. 2010; Schilling et al. 2016; Souza et al. 2019). Litterfall in CAF, SAF, and CM (range: 5.07 – 6.23 Mg ha^{-1} yr^{-1}) was similar to values found in other cacao production systems (range: 4 – 8 Mg ha^{-1} yr^{-1}) in Central Sulawesi, Indonesia, and Brazil (Fontes et al. 2014; Tridiati et al. 2011), and marginally higher than values for cacao agroforestry systems in Nigeria and Bolivia (Muoghalu and Odiwe 2011; Schneidewind et al. 2018), but lower than for cacao agroforestry systems in Cameroon (Saj et al. 2021).

As expected, we found a seasonal pattern in litterfall across the land-use gradient, with overall higher litterfall during the dry season, similar to results for cacao-based land-use systems in Ghana (Dawoe et al. 2009). Similar patterns are also found in natural forests, for example, for forests in Tanzania where litterfall was closely related to seasonal variation in rainfall (Becker et al. 2015). Litterfall increased significantly in the dry months (monthly precipitation < 150 mm), which indicates that a physiological response to drought plays a significant role. During the dry season, trees shed more leaves to reduce evapotranspiration due to low soil water availability.

Contrasting decomposition rates across the land-use gradient: strong effects of inherent litter quality

Both inherent litter quality and microclimatic variation across the land-use gradient were expected to

drive decomposition rates in the cacao agroforestry landscape. By examining the decay rates of litter originating from different land-use systems, we evaluated the effects of litter chemistry and land-use system on decomposition. Decomposition rates in our study (Table 2) were generally lower than those found in a cacao agroforestry study in Central Sulawesi, Indonesia (Tridiati et al. 2011), and in a cacao plantation in Nigeria (Muoghalu and Odiwe 2011), probably due to differences in litter quality. The low decomposition rate that we found results in a longer litter residence time, which could be beneficial to maintain soil cover, and enhance soil surface protection from erosion (Hairiah et al. 2006). On the other hand, slower nutrient release decreases nutrient inputs to the soil.

We found that litter quality was a stronger driver of decomposition rates than microclimate and HFA, which aligns with results from previous studies (Dawoe et al. 2009; Fontes et al. 2014; Hoeber et al. 2020; Zhang et al. 2008). The decomposition process in our study was controlled by the ratio of (L+Pp):N. (L+Pp):N index may be the best predictor of decomposition rates in agroforestry systems, because including an estimate of protein binding capacity (Pp) in the litter quality index improves the prediction (Mafongoya et al. (1997). Chemical reactions between Pp and proteins and N generates condensed tannins, which slow down decomposition and nutrient dynamics (Mohan Kumar 2007; Waterman and Mole 1994). In our study, the effect of microclimate on decomposition rates was less profound, as is often found in tropical climates (Bargali et al. 1993; Couteaux et al. 1995). The relatively small contribution of HFA in our study agrees with results of Fanin et al. (2016) that the microbial communities and its interactions with the substrate explain just a small part of the variation in decomposition (<5%) across a land-use gradient (deciduous forest, tree plantation, grassland and cropland).

We found a positive HFA value in SAF, but a negative to zero HFA value in RF, CAF, and CM, which aligns with results of recent studies in a coffee based agroforestry system and botanical garden in Indonesia (Hairiah et al. 2021; Rachmawati et al. 2019). A positive HFA value indicates that litter from SAF decomposed faster by the microbial community in its original environment compared to other environments probably because the microbial community is adapted to the local litter characteristics (Ayres et al. 2009; Veen et al. 2015). Nevertheless, faster decomposition in SAF, also for litter originating from other land-use systems, might also be due to higher soil moisture, supporting soil organisms to accelerate the decomposition process. The moderate tree density in SAF increases soil water content, compared to CAF and CM (Saputra et al. 2020).

Effect of decomposition rates on soil C and N change

We expected the relative change of soil C and N during litter decomposition to vary across land-use systems, litter origin, and over time, with a positive relationship between the decomposition rate and the change of soil C and N. Overall, we did not consistently find that faster decomposition rates increased both the relative change of soil C and N content. The variation in soil C and N change was mostly explained by land-use system, thus representing the environmental conditions in which the decomposition occurs (e.g. including soil characteristics, microbial communities). Soil characteristics may play more important role as a driver of soil C and N changes than the litter type which represent the quality of the litter. In term of soil nutrient, soil characteristics such as microbial communities and chemical properties had a higher positive effect on soil C and N contents than litter quality during litter decomposition (Delgado-Baquerizo et al. 2015). We acknowledge that the change of soil C and N content in our study was larger than expected, which might be due to an additional input of organic matter from another pool such as old roots that were present in the land-use system still after previous land use.

Surprisingly, we found that the relative change of soil C and N content under SAF litter in its original environment was the highest compared to other treatments at the end of the experiment. This result supports our finding of the effect of HFA that has been found in SAF, where the decomposition rate was higher in the original/home environment than in the other land-use systems. A combined effect of good adaptation of the microbial community to the local litter characteristics and appropriate soil moisture may accelerate the decomposition process. Adequate soil moisture and temperature in SAF (Fig. 2) may be optimal for the soil microbial community, accelerating decomposition which possibly results in a higher C and N release to the soil. Faster decomposition

increases nutrient release into the soil and increases soil nutrient levels (Zhang et al. 2018; Zhang et al. 2016). Conversely, 'unfamiliar' organic material addition, especially with low soil moisture may inhibit microbial activity (Borowik and Wyszkowska 2016) by reducing diffusion of soluble substrates, activity of enzymes and intracellular water potential (Stark and Firestone 1995), limiting substrate degradation, which may result in the lower change of soil C and N in the other treatments.

Generally, the relative change of N content beneath the litter types placed in the land-use systems was negative during the first week. Therefore, soil N concentration under litter from RF, CAF, and CM declined during the first week. A 'delayed' priming effect might have occurred after the addition of low-quality litter (Fanin et al. 2020), where soil microbes acquire N from the soil to be able to decompose the low-quality material, resulting in a decrease in soil N. At this point, soil microbes start mining N from the soil to invest energy to break down organic matter (Talbot and Treseder 2012).

Species mixtures of pruning residues modify decomposition rates, net N litter loss, and soil C and N change

In addition to litterfall, pruning residues are an essential source of organic matter input in agroforestry systems. Compared to the decay rate of existing standing litter; fresh pruning residues decomposed slightly faster due to the lower (L+Pp):N ratio (Table 2). As we expected, we found non-additive effects of the litter mixture since the decomposition rate of mixed pruning residues was not equal to the mean decomposition rate of the two single species together, involving both synergetic and antagonistic responses (Gartner and Cardon 2004). Mixed pruning residues of cacao and *Fagraea fragrans* accelerated the decomposition rate relative to the mean decomposition rate of the two single species together, representing the occurrence of synergetic responses. Our result agrees with results of a recent global decomposition study that the mixture of low-quality litter showed a significant synergetic effect (Liu et al. 2020). A similar pattern was found for the mixture of cacao and *Gliricidia* compared to cacao alone, with up to 30% higher mass loss for the species mixtures (Hoorens et al. 2010; Tardif et al. 2014). Adding *Gliricidia* to cacao could increase the decomposition rate, because *Gliricidia* has higher litter quality. When litter of different species is mixed, high-quality litter brings more accessible carbon to support microbe growth (Hättenschwiler and Jørgensen 2010). In this case, microbial activity, and extracellular enzyme activity, which are responsible for substrate degradation, increase simultaneously (Eisenhauer et al. 2011; Gogo et al. 2016), triggering faster decomposition. However, when comparing a cacao and *Gliricidia* mixture with *Gliricidia* leaves alone, the decomposition rate of litter mixture became lower since *Gliricidia* leaves had the highest decomposition rate.

We found that the total amount of net N loss from mixed pruning residues was inconsistent over time. In some cases, net N loss from mixed pruning residues was significantly higher compared to the mean value of both single-species pruning residues together, particularly for the combination of cacao and *Gliricidia*. The addition of high-quality litter (*Gliricidia*) contributes more available N for soil microorganism, triggering an 'immediate' priming effect (Fanin et al. 2020). In other cases, when the relative net N loss of mixed pruning residues was lower than the mean N loss of the two single species together, the amount of its N loss was determined by the species with higher litter quality. This may indicate that high-quality material could stimulate the decomposition of more recalcitrant litter types (Gartner and Cardon 2004).

The relative change of soil N content in both mixed litter combination was slightly higher than for cacao leaves alone. This may occur because of mixed pruning residues that decomposed faster than single cacao leaves. We found a significant increase of the relative change in soil N, with the amount of N loss from the pruning residues across all treatments and land-use systems, thus pruning residues of cacao and shade trees increased soil N. The N-fixing tree species *Gliricidia* strongly increased soil N content, as the relative increase in soil N was highest under pruning residues of *Gliricidia* (Fig. 6b). In cacao-based agroforestry systems in Bolivia, the presence of the N-fixing legume tree *Erythrina spp.* (L.), which is often planted as a shade tree in cacao production systems, increased soil N content and N uptake by cacao trees (Schneidewind et al. 2018). The presence of N-fixing trees in agroforestry systems is essential, particularly on N-poor soils, as it decreases the need for fertilizer input (Schroth et al. 2001).

Persistence of the litter layer over time: implications for the management of cacao-based agroforestry systems

The dynamics of the standing litter stock represents the balance of litterfall and its decomposition rates. Remnant forests were expected to have a permanent litter layer and annual crop systems bare soil over time. For cocoa production systems, we expected the balance between litterfall and decomposition to depend on the characteristics of the land-use systems that influence litterfall and decomposition. We found distinct temporal patterns of standing litter stocks in remnant forest and cacao production systems throughout the year, with generally higher standing litter stocks in the dry season. Low moisture content during the dry season reduces soil organism activity and could decelerate the decomposition process (Siebert et al. 2019), resulting in higher standing litter accumulation. Higher litterfall during the dry season might further increase litter stocks. In RF, a significant input of low-quality, slow-decomposing litter during the dry season resulted in more litter accumulation on the forest floor. CAF and CM had a relatively long litter residence time (more than a year), which indicates that the current litter layer is sufficient to maintain permanent soil cover to protect the soil surface from erosion and direct heating. The low quality of CAF and CM litter may delay the nutrient release, which slows down the nutrient supply to the soil. In contrast, the shorter litter residence time in SAF (less than a year) is likely to promote higher nutrient availability into the soil but can cause soil surface exposure and nutrient loss (through leaching or volatilization) due to the rapid decomposition rate if N mineralization is not synchronized with plant growth. However, in the case of mixed system, shade trees in agroforestry systems have diverse root systems, which can increase the buffer capacity to capture nutrient loss (van Noordwijk and Cadisch 2002).

Managing pruning residues is important to optimize system functioning (to cover the soil surface, regulate litter decomposition rates, and supply nutrients to the soil). Slowly decomposing pruning residues could be added to cacao agroforestry systems with fast-growing shade trees at the beginning of the rainy season to increase soil protection from the direct splash impact of the rain. On the other hand, low-quality material addition would delay the decomposition rate of high-quality litter, preventing nutrient loss from the system. For cacao agroforestry systems with slow-growing shade trees, adding high-N *Gliricidia* litter at the end of the rainy season (when litterfall starts to increase) could increase the decomposition rate, triggering higher nutrient release to the soil. In the longer term, increasing shade tree diversity in a cacao production system with large variation in litter quality would be beneficial for achieving multiple objectives from both the ecological and production perspective. Wartenberg et al. (2019) evaluated the effect of shade trees on cacao production in the same study site and found that the presence of shade trees could increase soil nutrient levels. Simple agroforestry systems likely perform slightly better than complex systems in minimizing the trade-off between yield and nutrient competition (Wartenberg et al. 2019). However, in terms of litter persistence, complex agroforestry systems can maintain a permanent litter layer, ensuring soil protection and organic matter addition over the year. Additionally, sufficient moisture and decomposed organic substrate, which are contained in the litter layer, provide an optimal habitat for midges, which are crucial for cacao pollination (Tscharntke et al. 2011; Young 1982). This could serve to increase the cacao productivity in agroforestry systems (Toledo-Hernández et al. 2017). Managing complex agroforestry systems properly is essential to achieve sustainable production systems, with high potential for biodiversity conservation, carbon stocks, soil protection and nutrient cycling.

Conclusions

In conclusion, the seasonal pattern of litterfall production and relatively slow litter decomposition rates supported a permanent litter layer over the year in all cacao production systems and in the remnant forest. Inherent litter quality, as expressed by (L+Pp):N was the strongest driver of decomposition rates, while microclimate and HFA had only a weak effect. Low-quality litter from cacao production systems (CAF and CM) decelerated the decay rate and extended the litter residence time to over a year, ensuring protection of the soil surface from erosion and direct heating. Consequently, the C and N supply to the soil may be insufficient, as total soil C and N content was low. Conversely, faster-decomposing litter in SAF resulted in higher C and N release, but shorter litter

residence time, which could lead to increased soil surface exposure during the rainy season.

Management strategies involving transfer of pruning residues across cacao production systems could be optimized by considering the temporal pattern of standing litter stocks. Determining the precise timing for organic matter transfer is essential to improve efficiency and synchronization, particularly during the time when the soil surface is exposed, and soil nutrient content is low. Further research is needed on the long-term effect of different management strategies of the litter layer in cacao production systems, from an ecological and economic perspective on cacao production and its sustainability.

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Declarations

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

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