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The effect of *Jatropha curcas* L. leaf litter decomposition on soil carbon and nitrogen status and bacterial community structure (Senegal)

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The cultivation of *Jatropha curcas* L. as a biodiesel feedstock has been encouraged in Senegal to reduce dependence on fossil fuels and mitigate the effects of climate change. *J. curcas*is is a poisonous plant which sheds its leaves during the dry season. Although the leaves are toxic for animals, they can help to recycle soil organic matter. This study set out to determine the effect of the decomposition dynamics of green and senescent *J. curcas* leaves on the soil C and N contents and on the structure of the bacterial community. Leaf litter decomposition was studied for 4 months by laboratory incubation and samples were taken at the start of incubation and at 3, 28, 56, 90 and 120 days. Green leaves had a higher N content, higher concentrations of water soluble compounds and hemicelluloses, but a lower C:N ratio and lignin content than senescent leaves regardless of the cultivar. The cultivar, the type of litter and the interaction between them, all had a significant effect on the soil N content ($p<0.0001$, $R^2=0.995$) and C:N ratio ($p<0.0001$, $R^2=0.998$). However, the cultivar was the only factor that affected the leaf C content ($p<0.05$, $R^2=0.624$). The initial N content explained the $N\text{-}NH_4^+$ mineralization at the start of decomposition and the initial lignin content explained the $N\text{-}NH_4^+$ mineralization at later stages of decomposition. The recalcitrant C content in the green leaves was estimated as being between 70.01 and 73.33% of the total C content and between 72 and 77.33% in senescent leaves. This suggests that Jatropha litter may contribute significantly to soil C sequestration. The results indicate that the soil had higher bacterial diversity in the later stages of litter decomposition, for both types of litter and all cultivars.

Key words: *Jatropha curcas* L., leaf litter, nitrogen mineralization, carbon mineralization, bacterial community, polymerase chain reaction denaturing gradient gel electrophoresis (PCR-DGGE), Senegal.

INTRODUCTION

Soils in the arid and semi-arid Sudano Sahelian region of West Africa have an intrinsic low level of fertility (Bationo and Buerkert, 2001) and increasing pressure from livestock grazing is causing a significant loss of organic

matter and depletion of nutrient reserves in soils (Dossa et al., 2009). Organic matter input has been shown to be critical for improving soil quality and optimizing nutrient and water efficiency and ultimately crop productivity in these degraded agro ecosystems (Sinaj et al., 2001; Tschakert, 2004). The preservation of soil functions requires sustainable management of soil organic matter (SOM). Of the practices aiming to maintain and increase SOM, mulching with plant residues is beneficial as it improves soil fertility, increases carbon sequestration and provides sustainable recycling of organic residues.

In Senegal, the gradual depletion of world fossil fuel reserves and the inability to provide adequate energy services have led to the adoption of renewable energy sources. *Jatropha curcas L.*, an oil-yielding tropical plant, was considered to be a promising alternative to fossil fuels with high economic potential. Given this increased interest in *J. curcas* as a biodiesel feedstock, it was introduced in Senegal in 2007 and has since been cultivated intensely throughout the country, especially in rural areas. *J. curcas* is a perennial plant belonging to the Euphorbiaceae family with poisonous seeds and leaves. Wani et al. (2012) estimated that the accumulated leaf fall from a 3 to 5 year old *J. curcas* plantation added 1450 kg ha^{-1} of carbon to the soil, 800 kg of this from the leaves, suggesting that leaves can recycle soil organic matter and nutrients (Patrício et al., 2012).

However, little research has been carried out into *J. curcas* leaf litter decomposition processes and their role in the maintenance of soil and environmental functions. It has been established that litter decomposition and nutrient release is controlled by the chemical composition of the litter (Arriaga and Maya, 2007) as well as by abiotic factors and microbial activities (Li et al., 2011). Although the C:N ratio or N related indices of residues are often found to be the main factors governing decomposition processes (Kemp et al., 2003; Bray et al., 2012), other factors such as the lignin, cellulose, polyphenolic and tannin contents of the litter also affect nutrient release dynamics during decomposition (Zhang et al., 2008; Talbot and Treseder, 2012). Changes in the chemical composition of the litter have been found to affect the decomposition rates of different types of litter (Milcu et al., 2011) and to have a noticeable effect on the microbial decomposer community during the decomposition process (Bray et al., 2012; Knelman et al., 2012; Esperschütz et al., 2013; Pfeiffer et al., 2013). Microbial decomposer communities can change during litter decomposition owing to biotic interactions and shifting substrate availability (Chapman et al., 2013).

Recent studies have found out that changes in litter composition owing to decomposition can have a significant effect on microbial community composition and on ecosystem processes (Chapman et al., 2013). The cultivation of *J. curcas* modifies the fungal community structure, but does not have a specific, systematic effect on the structure of the soil bacterial community (Dieng et al., 2014). However, *J. curcas* may affect the structure of the soil bacterial community indirectly through litter decomposition. Further research is required into the mechanism of the decomposition of senescent or green *J. curcas* leaf litter and its potential or releasing nutrients and thus providing agronomic and environmental services.

This study investigated the effect of *J. curcas* leaves on the dynamics of soil C and N cycling and the structure of the bacterial community after the soil had been mulched with senescent and green leaves in laboratory conditions.

MATERIALS AND METHODS

Soil sampling

The site from which soil samples were taken was located in Goudiry, South East Senegal (14°11'15.27"N 12°42'44.79"W). The soil is hydromorphic ferruginous containing 6 to 9% clay, 0.90% total C, 0.08% total N and 7.9 mg g^{-1} total P and the pH is estimated at 6.17. Soil samples were collected in February 2010 from the 0 to 20 cm horizon. The samples were air dried in the laboratory and sieved through a 2 mm mesh prior to treatment and analysis.

Mozambic

Fresh green and senescent leaves were collected from the branches of two native and two introduced cultivars of *J. curcas* planted at the Higher National School of Agriculture, Thiès University (14°42'52''N, 16°28'64''W). This plantation was a completely randomized design with 4 cultivars. The spacing between plants was 2 m. No fertilizer was used for this experiment. The native cultivars selected were Banfadjiré (Ban) and MadiopBoye (MB) from Senegal and the introduced cultivars were from Mozambique (MOZ) and Tanzania (TZ) (Table 1). For each cultivar, leaves were taken from 4 plants (4 replicates) and mixed, air-dried at ambient temperature in the laboratory for 3 weeks and then sieved through a 2 mm mesh. The green leaf litter is indicated by a 1 (Ban1, MB1, MOZ1 and TZ1) and the senescent leaf litter is indicated by a 2 (Ban2, MB2, MOZ2 and TZ2) (Table 1).

Soil and litter incubation

Two sets of soil samples, 20 g for C mineralization and 40 g for N mineralization and bacterial dynamics, were used. The samples were pre-incubated at 28°C for one week to reactivate the microorganisms. The soil humidity was adjusted to 60% of water holding capacity during the pre-incubation phase and 80%

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thereafter. The litter was applied as a mulch on the soil surface at a rate of 508 kg ha^{-1} (Abugre et al., 2011). This was equivalent to the highest litter fall of *J. curcas* at a planting distance of 1 × 1 m during the dry season. Three replicates were taken for each type of litter. For C mineralization, samples were transferred to a 150 ml glass flask sealed with a septum and incubated at 28°C for 120 days. For N mineralization, each sample was incubated at 28°C in 500 ml glass flasks with 15 ml of 1 M NaOH as a CO_2 trap. Three flasks with soil and no litter were used as controls. Samples were taken at the start of incubation and at 3, 28, 56, 90, and 120 days for determination of the total soil C and N contents and an aliquot of each sample was stored at -20°C for DNA extraction later.

Chemical composition of soil and leaf litter

The water soluble compound, hemicellulose, cellulose and lignin contents were determined as described by Goering and Van Soest (1970). The total N and C contents were determined by dry combustion using a LECO FP 428 CHN autoanalyzer (LECO Corp, St. Joseph, Mich). The total P content was determined by colorimetry (Murphy and Riley, 1962). All C, N and P analyses were performed at the IRD LAMA laboratory (Laboratoire des Moyens Analytiques, certified ISO 9001 2008), Dakar, Senegal.

Carbon and nitrogen mineralization

Carbon mineralization was analyzed by measuring the CO_2 released during incubation. The air in the flasks was analyzed by injecting the gas directly from the flask into an MTI Analytical Instruments P200 gas chromatograph (Microsensor Technology, Fremont, Calif.) equipped with a TCD detector using helium as the carrier gas. The gas analyzer was used in combination with the Windows-based EZChrom 200 chromatography data system.

The mineral N was determined using KCl soil extracts (1 M KCl) by colorimetric flow injection analysis as described by Bremner (1965). Net N, $N\text{-}NH_4^+$ and $N\text{-}NO_3^-$ content were determined relatively to soil control.

Soil DNA extraction and polymerase chain reaction denaturing gradient gel electrophoresis (PCR-DGGE)

Soil DNA extraction

The soils used for DNA extraction were aliquots of the same soil samples used for mineralization analysis which had been stored at -20°C from each sampling day. DNA was extracted from 0.25 g aliquots of soil using Fast DNA Spin Kit for Soil (MP-Biomedicals, NY, USA) according to the manufacturer's instructions. The purified DNA was re-suspended in 100 µl of DNase-free water (MP-Biomedicals) and the DNA concentrations were quantified using a NanoDrop ND-1000 UV-Vis Spectrophotometer (NanoDrop Technologies, USA) according to the manufacturer's instructions. Three replicate DNA extractions from each sample were pooled prior to PCR amplification.

PCR-DGGE

The V3 region of the 16S rRNA gene was amplified for DGGE analysis using primers UNIV518r (Ovreås et al., 1997) and EUB338f with a 40-bp GC clamp at the 5' end (Muyzer et al., 1993). The reaction mixture of 25 µl contained 5 ng of DNA, Taq Polymerase Ready-To-Go (Amersham-Bioscienes, France) and 1 µM of each primer. The PCR was performed using the following program: initial denaturation for 5 min at 94°C, followed by 20 cycles of 30 s at 94°C (denaturation), 1 min at 65°C (annealing) with a 0.5°C touch down every second cycle, and 1 min at 72°C (elongation), followed by 10 cycles with an annealing temperature of 55°C and a final cycle of 10 min at 72°C. The PCR products were separated by electrophoresis in 1.5% (w/v) agarose gels and stained for 30 min with ethidium bromide (1 mg L^{-1}). 20 µl of the PCR products were separated using the Ingeny U-Phor system (Ingeny, Goes, The Netherlands) in 8% polyacrylamide (acrylamide–bisacrylamide [37.5:1]) gel with a linear 45 to 70% denaturant gradient (100% denaturant containing 7 M urea and 40% formamide). Electrophoresis was carried out using a 1X Tris-acetate-EDTA buffer at 100 V and 60°C for 17 h. The gels were stained for 30 min with ethidium bromide (1 mg L^{-1}) and de-stained in distilled water for 10 min. The bands were then photographed using a Vilber Lourmat imaging system (EtsVilberLourmat, France). Band detection and intensity quantification were performed using Total Lab gel imaging software (Nonlinear Dynamics Ltd., Newcastle UK), with manual checking and adjustment of each band position. The band intensity was used as an indication of relative abundance.

Statistical analysis

The N and C contents and C:N ratio were analyzed by two way analysis of variance (ANOVA) and the means were assessed using Fisher's Least Square Difference (LSD) test at 95%. A one way ANOVA was performed to assess the difference between the mineral N for each treatment. A Pearson test at 95% was used for all correlation tests. All analyses were performed using XLSTAT-Pro (AddinSoft, v10, France).

The net CO_2 emitted by the mulched samples was obtained by subtracting the CO_2 emitted by the controls and C loss was calculated as the net CO_2 divided by the initial litter carbon content. The carbon loss data were also fitted to the double exponential decomposition model of Wider and Lang (1982) used in previous studies (Beyaert and Voroney, 2011; Staelens et al., 2011; Patrício et al., 2012).

$$Ct = C1e^{-k1t} + C$$

where Ct is the % of carbon remaining at time t, C1 is the initial % of component 1 (labile C) at the start; k_1 is the decomposition rate for labile C; C2 is the initial % of component 2 (recalcitrant C) at the start, and k_2 is the decomposition rate for recalcitrant C.

The 16S rDNA-DGGE banding patterns were scored by the presence/absence of bands using the Dice index. Phoretix 1D (TotalLab Ltd) was used to cluster the patterns using the unweighted pair group method with mathematical average (UPGMA). The structural diversity of the bacterial community was estimated using the Shannon index of general diversity based on the number of bands and the relative intensity of the bands in each lane. The intensity of the bands was estimated from the peak heights. The Shannon H index was calculated using the following equation:

$$H = -\sum (Pi \times \log Pi)$$

where Pi is ni/N, ni is the peak height and N is the sum of all peak heights.

To show the overall differences, Principal Component Analysis (PCA) was performed on a data matrix of various variables (mineral N, soil C/N ratio, cumulative CO_2 and Shannon diversity) using the

Table 1. Litter origin and chemical characteristics.

Origin	Litter type	Treatment	Total N (%)	Total C (%)	C/N	WSC	HEM	CEL	LIG
Banfadjiré (Senegal)	Green	Ban1	3.09 (0.09)	44.66 (0.68)	14.44 (0.24)	46.6	10.7	18.8	12.3
	Senescent	Ban2	1.69 (0.02)	45.34 (0.50)	26.75 (0.51)	38.6	4.1	21.3	24.8
MadiopBoye (Senegal)	Green	MB1	2.85 (0.09)	43.27 (0.37)	15.19 (0.54)	47.0	10.9	17.5	11.7
	Senescent	MB2	1.46 (0.05)	44.81 (0.94)	30.75 (0.48)	38.1	6.9	17.1	22.7
Mozambic	Green	MOZ1	3.11 (0.02)	44.22 (0.46)	14.24 (0.11)	44.3	6.1	11.9	25.9
	Senescent	MOZ2	1.33 (0.02)	43.60 (0.15	32.78 (0.63)	29.0	3.8	26.5	27.8
Tanzania	Green	TZ1	2.95 (0.07)	44.87 (1.01)	15.19 (0.07)	48.8	10.9	15.7	12.3
	Senescent	TZ2	1.70 (0.05)	45.16 (0.63)	26.52 (0.54)	40.0	7.5	18.9	23.0

Table 2. Two ways ANOVA (origin and litter type) on C, N and C/N ratio litter contents.

Variation sources	Statistical parameters	N total	C total	C/N
Model	R^2	0.995	0.624	0.998
	F	478.920	3.794	965.156
	Pr > F	<0.0001	0.013	<0.0001
Origin	F	17.883	4.983	65.693
	Pr > F	<0.0001	0.013	<0.0001
Litter type	F	3.240.771	3.144	6.314.537
	Pr > F	<0.0001	0.095	<0.0001
Origin×litter type	F	19.341	2.822	81.492
	Pr > F	<0.0001	0.072	<0.0001

XLSTAT, PCA option (XLSTAT version 10, Addinsoft, France).

RESULTS

Chemical composition of the litter

The chemical characteristics of the leaf litter are shown in Table 1. For green leaves, Ban1 and MOZ1 had a significantly higher N content ($p < 0.0001$) than TZ1 and MB1. For senescent leaves, MOZ2 had the lowest N content ($p < 0.0001$). The C content of Ban and TZ was significantly higher ($p < 0.05$) than MB and MOZ indicating that the cultivar had a significant effect ($p < 0.05$) on the leaf C content (Table 2). For all cultivars, the C:N ratio was significantly higher ($p < 0.0001$) in senescent leaves (1.7 to 2.2 times higher) than in green leaves. Senescent leaves from MOZ hadt he highest C:N ratio (32.78) followed by those from MB (30.75). Water soluble compounds and hemicellulose content were higher in the green leaves than in the senescent leaves while the senescent leaves had a higher lignin content. Senescent leaves had the highest cellulose content. MOZ1 leaves had high lignin and low cellulose and hemicelluloses contents. Two way ANOVA showed that the type of leaf litter, the cultivar and interaction between them, all had a significant effect ($p<0.0001$) on the soil N content and C:N ratio (Table 2). Green leaves had a higher N content than senescent leaves ($p < 0.0001$) for all cultivars.

C-CO_2 flux and carbon loss during decomposition

The C-CO_2 flux was higher in the early stages of incubation and was significantly higher ($p<0.0001$) for all mulched soils than for the control (Figure 1). The CO_2 flux in soils mulched with green leaves (0.14 to 0.15 mg g^{-1} day^{-1}) was higher than in soils mulched with senescent leaves (between 0.11 and 0.12 mg g^{-1} day^{-1}) after 3 days for all cultivars. However, there was no significant difference thereafter. The CO_2 flux after 3 days was positively correlated with the initial N ($p<0.0001$,

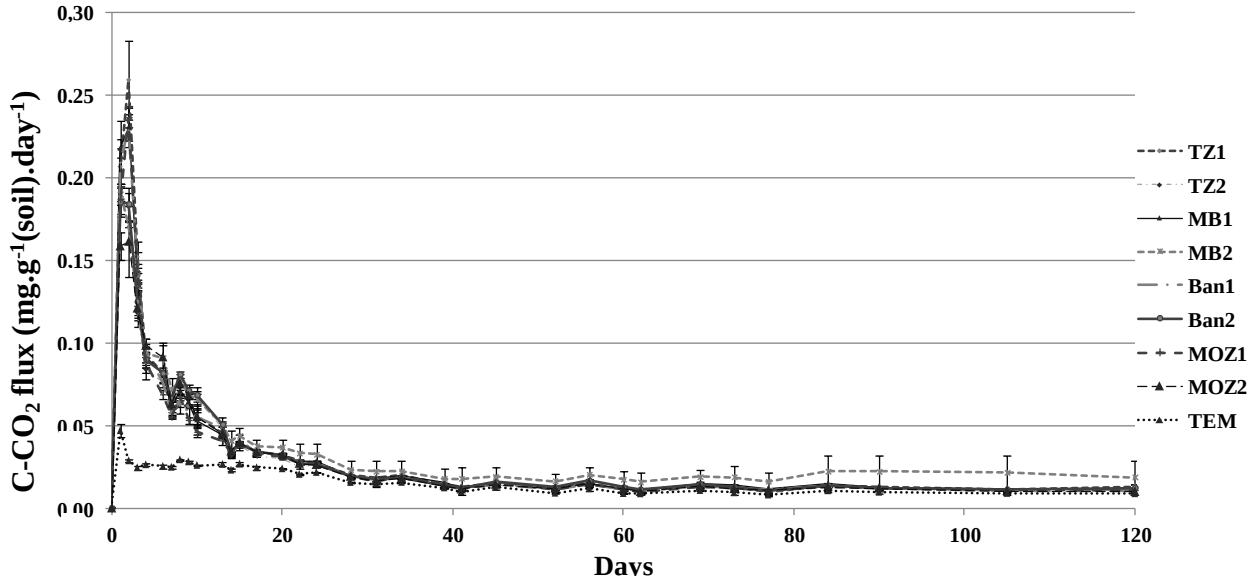

Figure 1. C-CO_2 flux (mg.g^{-1}.day^{-1}) of soil under litter supply by TZ1 and TZ2 (Tanzania), MOZ1, and MOZ2 (Mozambic), Ban1 and Ban2 (Banfadjiré) and MB1 and MB2 (Madiop Boye).

R^2=0.946) and negatively correlated with the C:N ratio (p=0.0003, R^2=0.90). At the end of experiment (120 days), there was no difference in the CO_2 flux (p<0.0001) between mulched soils and the control. The C loss data for the mulched soils was a good fit with the double exponential decomposition model (Figure 2) with R^2 varying between 99 and 99.9% (Table 3). In this model, carbon is separated into 2 compartments with different decomposition dynamics: labile and recalcitrant compounds. Labile C was decomposed rapidly (Table 3). The labile C decomposition rate k_1 was not significantly different between leaves from different cultivars but was significantly higher (p <0.05) for green leaves than for senescent leaves. Recalcitrant C was decomposed very slowly with a decomposition rate k_2 which was similar for all except MB1 and MB2. MB1 and MB2 were significantly different from TZ (*p*=0.044) and MOZ (p=0.04). The decomposition rate k_1 was negatively correlated with the initial cellulose content (p <0.05, R^2=0.707), whereas k_2 was not correlated with the initial content of any chemical compounds.

Nitrogen mineralization

The N-NO^-_3 release rate from the soil differed significantly during the incubation period (Figure 3). In TZ1, TZ2 and MB2, N-NO^-_3 was immobilized in the early stages of incubation, at 3 days. After 28 days, N-NO^-_3 was being immobilized in TZ1, TZ2, MB1 and MB2, the highest rate being in TZ2 (-21.8 µg g^{-1} soil). From 56 to 120 days, N-NO^-_3 was mineralized in all mulched soils except TZ2, where N-NO^-_3 was still being immobilized. The highest nitrification rate was in Ban1 during the incubation period except at 90 days when it was declining for both types of litter and all cultivars.

There were significant differences in the dynamics of N-NH_4^+ release during the incubation period (Figure 4). From day 3 to day 28, N-NH_4^+ was immobilized in TZ2, MB2, Ban2 and MOZ1. From day 56 to day 120, there was net ammonification in TZ1 and Ban1, while there was net N-NH_4^+ immobilization in all other mulched soils with the highest rate in MOZ1 (Figure 4). Finally, from day 28 to the end of the incubation, the highest net N mineralization was in Ban1, and the highest N immobilization was in TZ2 (Figure 5).

The N mineralization rates were correlated with the chemical composition. The N-NH_4^+ mineralization rate at day 3 was positively correlated (R^2=0.53, p<0.05) with the total N content of the litter and negatively correlated with the lignin content at day 28 (R^2=0.62, p<0.05), day 56 (R^2=0.53, p<0.05) and day 90 (R^2=0.62, p<0.05). The lignin content of the litter explained the change in net N mineralization at day 90 (R^2=0.54, p<0.05). PCA showed that during decomposition the net mineral N (N-NH_4^+ + N-NO^-_3), content of the soil was negatively correlated with the C:N ratio of the soil (Figure 6).

Bacterial DGGE banding patterns

Cluster analysis of DGGE banding fingerprints gave a

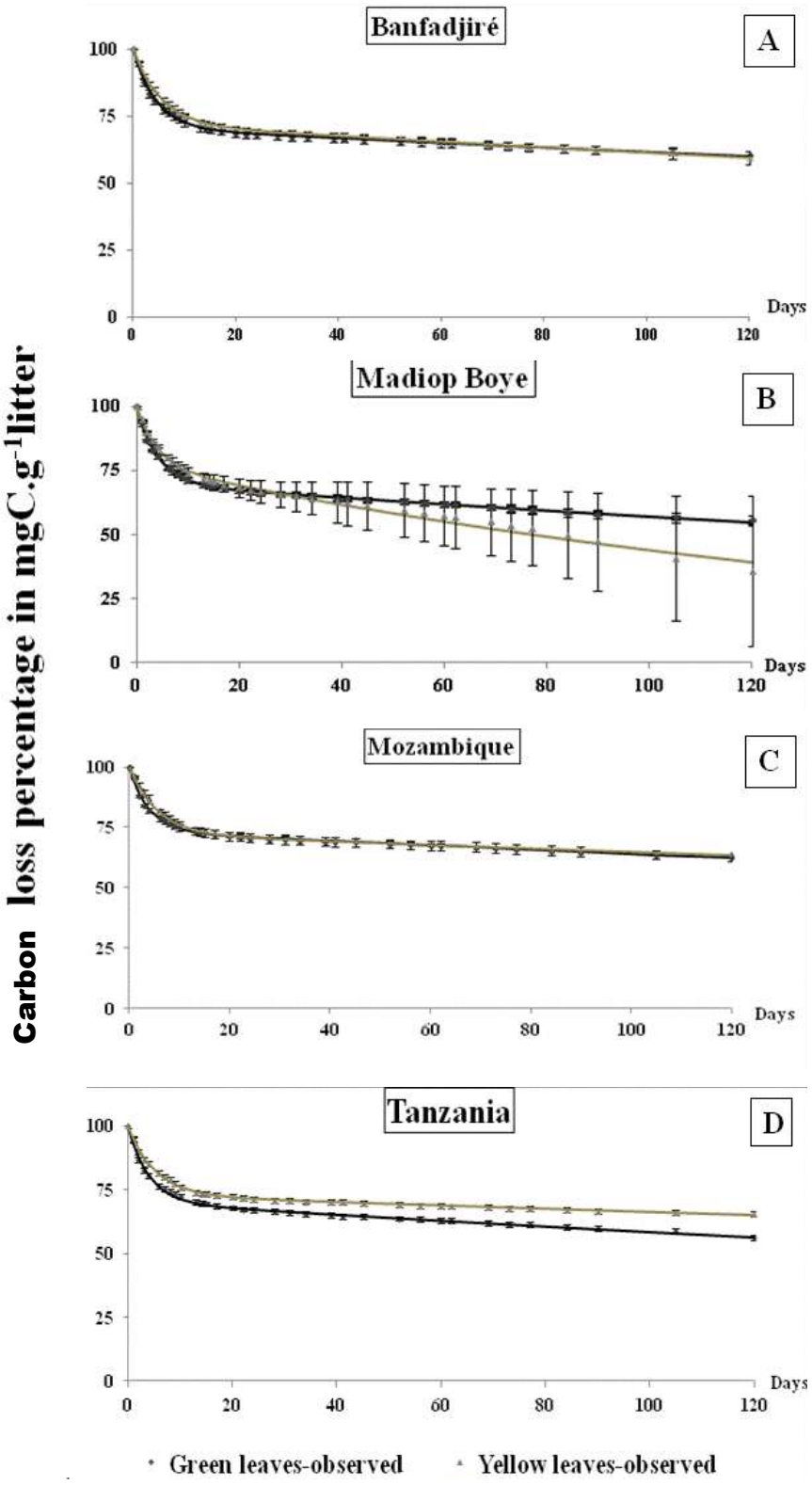

Figure 2. Percentage of Carbon remaining mass (mgC.g-1 litter) of treatment Banfadjiré (A), Madiop Boye (B), MOZ (C) and TZ (D) during green and senescent (yellow) leaves decomposition; dots are observed values (bars=standards deviation) and lines are expected values.

Table 3. Carbon loss model parameters with k_1 the decay constant rate of labile carbon and k_2 decay constant rate of recalcitrant C with standard deviation of green and senescent leaves.

Litter type	Origins	k_1 (day^{-1})	k_2 (day^{-1})	Labile carbon (%)	Equations	R^2
Green leaves	Banfadjiré	0.23 -0.019	0.001 (0.0002	29.39 -1.7	$Ct = 29.39e^{-0.23t} + 70.61e^{-0.001t}$	0.995
	Madiopboye	0.24 -0.001	0.002 -0.0002	29.99 -1.09	$Ct = 29.99e^{-0.24t} + 70.01e^{-0.002t}$	0.998
	Mozambica	0.25 -0.009	0.001 -0.0002	26.67 -1.92	$Ct = 26.67e^{-0.25t} + 73.33e^{-0.001t}$	0.99
	Tanzania	0.25 -0.012	0.002 -0.0001	29.77 -1.65	$Ct = 29.77e^{-0.25t} + 70.23e^{-0.002t}$	0.997
Senescent leaves	Banfadjiré	0.19 -0.015	0.002 -0.0003	28 0.43	$Ct = 28e^{-0.19t} + 72e^{-0.002t}$	0.999
	MadiopBoye	0.26 -0.073	0.006 -0.005	22.67 -4.58	$Ct = 22.67e^{-0.26t} + 77.33e^{-0.006t}$	0.991
	Mozambica	0.18 -0.008	0.001 -0.0002	27.8 -1.14	$Ct = 27.8e^{-0.18t} + 72.2e^{-0.001t}$	0.99
	Tanzania	0.19 -0.006	0.001 -0.0002	27.26 -0.47	$Ct = 27.26e^{-0.19t} + 72.74e^{-0.001t}$	0.998

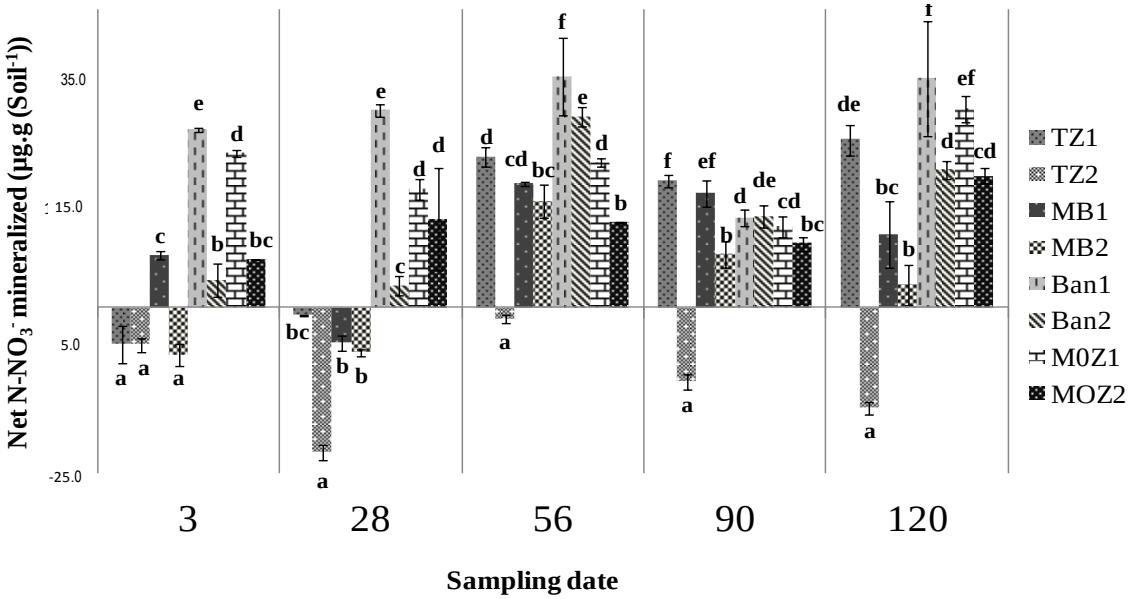

Figure 3. Net $N\text{-}NO^-_3$ mineralized under soil incubated with TZ1 and TZ2 (Tanzania), MOZ1 and MOZ2 (Mozambic), Ban1 and Ban2 (Banfadjiré), MB1 and MB2 (Madiop Boye).

dendrogram with 2 separate clusters with 72% similarity (Figure 7). The DGGE banding patterns at 0, 3, 28 and

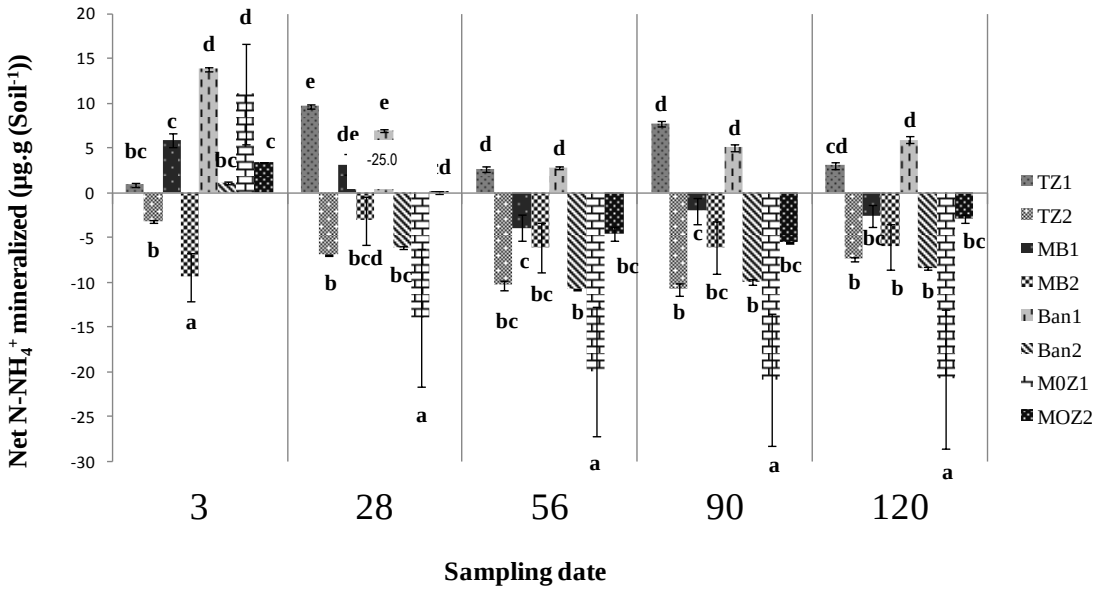

Figure 4. Net N-NH_4^+mineralized soil incubated with TZ1 and TZ2 (Tanzania), MOZ1 and MOZ2 (Mozambic), Ban1 and Ban2 (Banfadjiré), MB1 and MB2 (Madiop Boye).

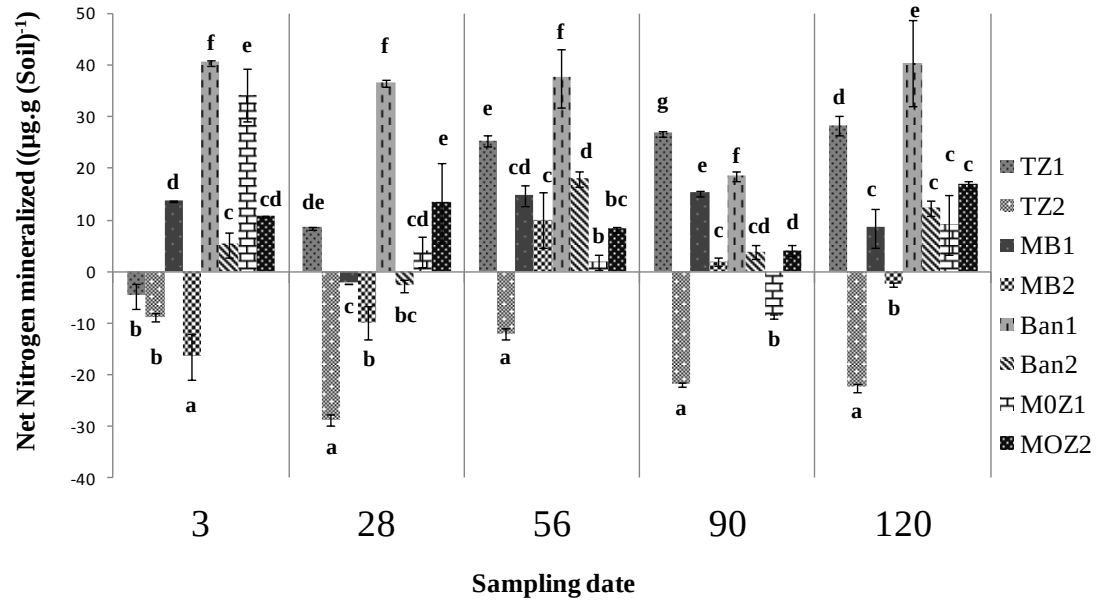

Figure 5. Net soil N mineralized under soil incubated with Jatropha green and senescent from Tanzania (TZ1, TZ2), Mozambic (MOZ1, MOZ2), Banfadjiré (Ban1, Ban2) and Madiop Boye (MB1, MB2).

56 days were clustered in Cluster I, whereas Cluster II comprised patterns at 90 and 120 days. Cluster I was divided into 2 sub-clusters (A and B) with 76% similarity comprising DGGE patterns at 0 and 3 days (sub-cluster A) and at 28 and 56 days (sub-cluster B). In sub-cluster A, day 0 had 88% similarity with day 3 (Figure 7). UPGMA analysis showed that for both types of litter and all cultivars, the bacterial community patterns for the various soils were clustered according to the litter decomposition stage. The Shannon diversity index (H)

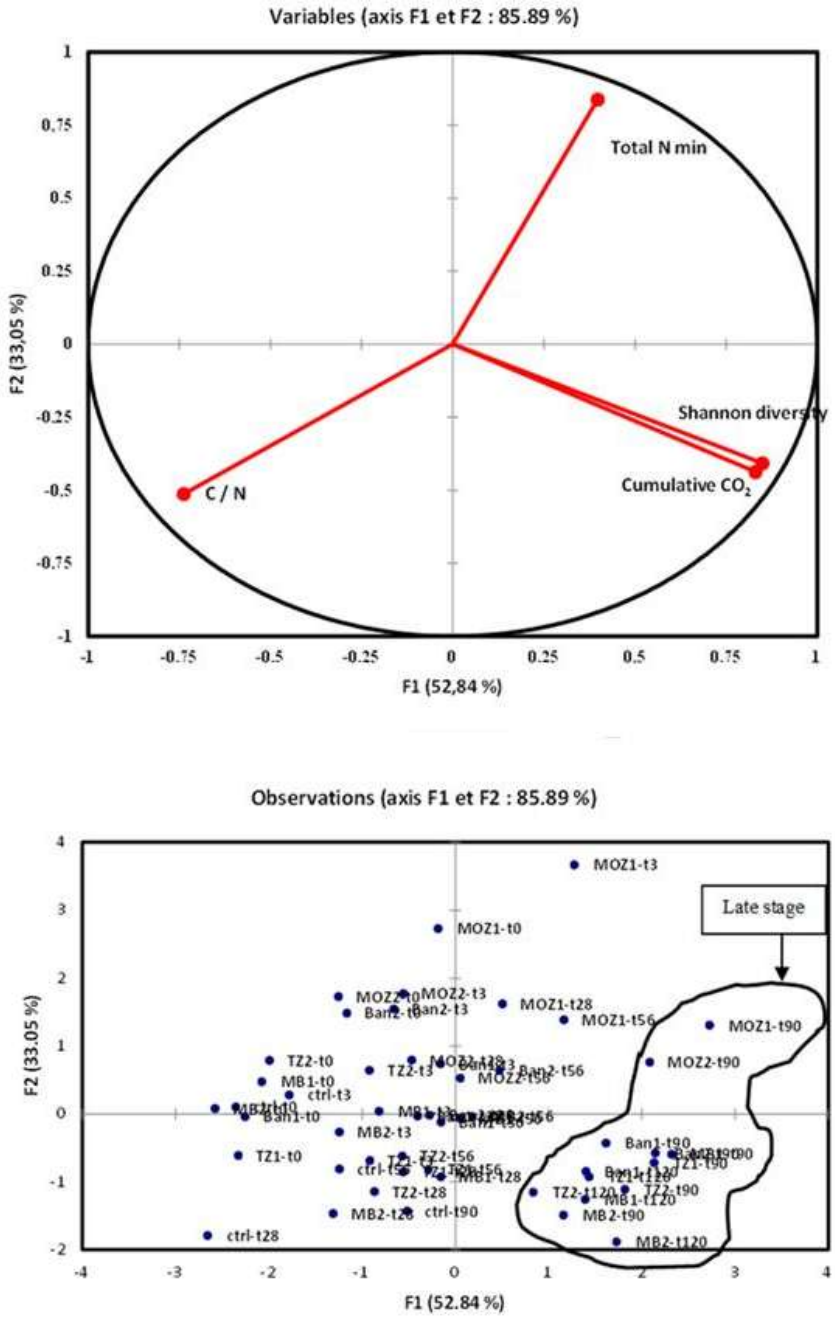

Figure 6. Principal Component Analysis of Shannon diversity, mineral nitrogen, C/N ratio and cumulative CO_2 on factorial plan F1-F2 (Ban=Banfadjiré; MB=Madiop Boye; TZ=Tanzania; MOZ=Mozambic; 1 = green leave; 2= senescent leave).

showed that the bacterial diversity increased significantly towards the end of incubation (Figure 6) and was correlated with the cumulative CO_2 indicating that the mulch had affected the bacterial diversity (Figure 6). However, the bacterial diversity and cumulative CO_2 were negatively correlated with the soil C:N ratio (Figure 6).

DISCUSSION

Chemical composition of *J. curcas* litter

This study showed that the chemical composition of *J. curcas* leaves depended on the cultivar. The

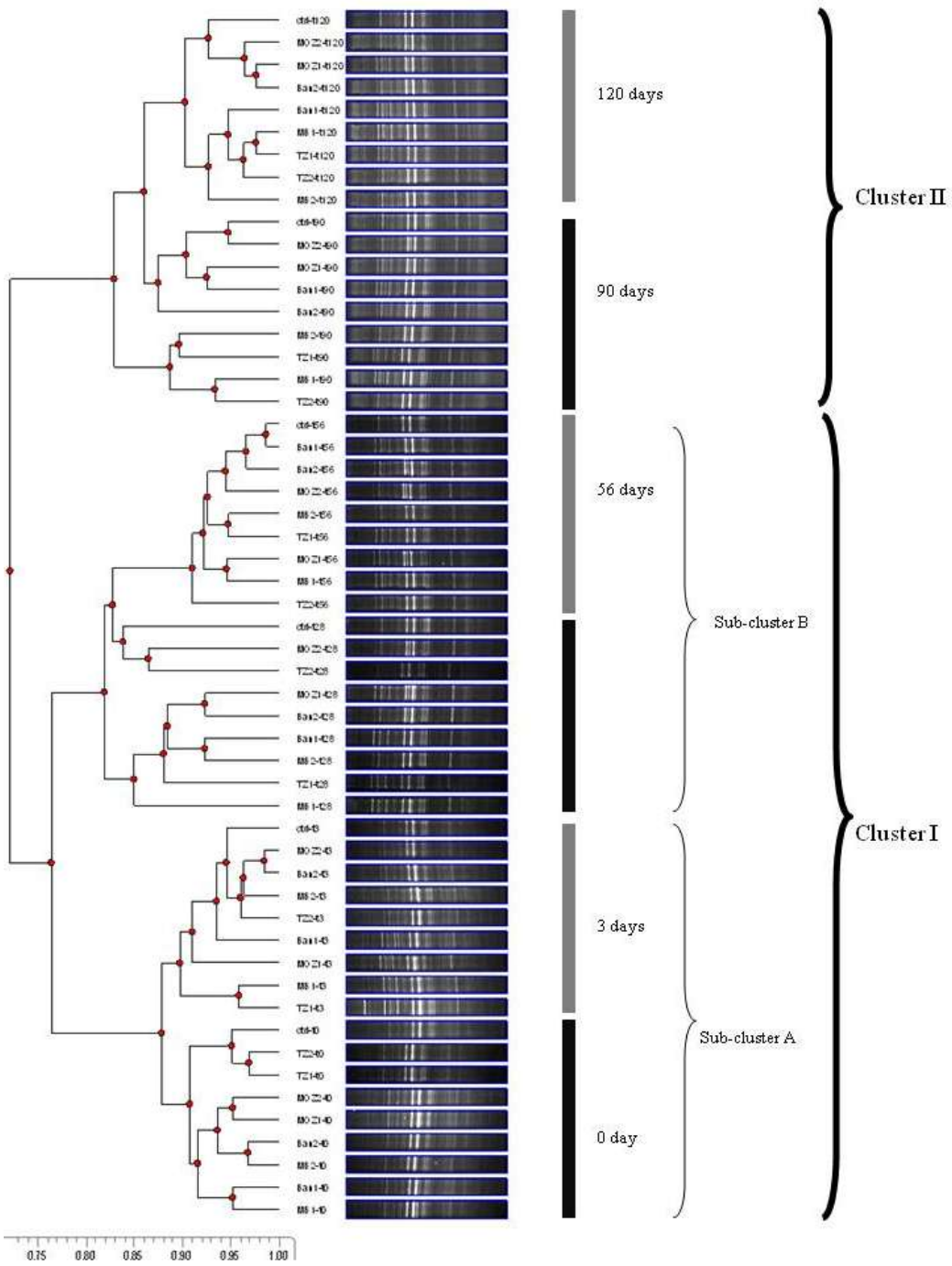

Figure 7. UPGMA clustering of soil DGGE fingerprints at 0, 3, 28, 56, 90 and 120 days after incubation. Ban = Banfadjiré; MB = Madiop Boye; MOZ=Mozambic; TZ=Tanzanian; Ctrl=control; 1 = green and 2 = senescent leaves.

geographical diversification of *J. curcas* has been found to affect the intraspecific variation of the plants and the leaf traits (Lecerf and Chauvet, 2008; Tanya et al., 2011) which confirmed that the phenotypic plasticity of *J. curcas* allows the expression of different phenotypes in response to changing environments (Heil, 2010). The lignin, C and N contents in the leaves has been shown to depend on the cultivar (Hättenschwiler et al., 2008). The lignin

content of green leaves was similar to that reported by Abugre et al. (2011) but was higher than that reported by Chaudhary et al. (2014). These biochemical differences could be explained by the intraspecific diversity of *J. curcas*. These findings agree with the findings of several authors (Lecerf and Chauvet, 2008; Petrakis et al., 2011; Zimmer et al., 2015) indicating that the intraspecific variation of leaf litter characteristics depends on environment rather than genetic background.

The lower N content in senescent leaves than in green leaves appeared to be the result of N resorption. As a drought-resistant perennial tree, *J. curcas*, resorbs the leaf macronutrients before shedding its leaves in the dry season. Nutrient resorption is a process in which nutrients, especially macronutrients, are transferred from leaves to other plant compartments before shedding (Wright and Westoby, 2003). The lower N nutrient content of senescent leaves for MOZ2 compared to those for Ban2 and MB2, indicated variation in N nutrient resorption. This result suggests intraspecific variation in the resorption process confirming the results obtained by Ramírez-Valiente et al. (2010). This finding is important for understanding the contribution of *J. curcas* leaves to soil nutrient inputs, because the different concentrations of nutrients in senesced leaves will affect litter quality and thus litter decomposition rates (Kitayama et al., 2004; Wardle et al., 2009; Hayes et al., 2014).

Modeling C decomposition rate and C sequestration

The double exponential decomposition model was a good fit with C mineralization data. It showed that C was divided into 28% labile C and 72% recalcitrant C. The decomposition rate for the labile component (k_1) was higher than that for the recalcitrant component (k_2) which agrees with the litter decomposition dynamics reported by Patrício et al. (2012). The rate of decomposition of recalcitrant compounds plays a key role in organic matter sequestration. In comparison to other published dynamics, *J. curcas* L. litter may, therefore, be considered as a slow decomposing litter, confirming its potential for sequestering C and improving soil fertility (Vauramo and Setälä, 2011).

The results showed that the labile C fraction and decomposition rate k_1 depended on the type of litter. Although the decomposition rates k_1 and k_2 were not correlated with the lignin content, k_1 was negatively correlated with the cellulose content ($p<0.05$, $R^2=0.707$), which implies that an increase of cellulose content in *J. curcas* leaf litter leads to a decrease in the decomposition rate of labile C. Different leaf litters decompose at different rates and it has been established that the initial chemical composition of the litter plays an important role in the decomposition rates. In this study, green leaf litter decomposed faster than senescent leaf litter which agrees with Li et al. (2011) who reported that increased nutrient availability, in particular N, stimulated litter decomposition. Therefore, it was not surprising that the decomposition rate was significantly higher in green leaves than senescent leaves ($p <0.05$).

It has been proposed that the composition of the soluble fraction, hemicellulose, cellulose and lignin compound are good indicators of the decomposition dynamics of organic residues (Lecerf and Chauvet, 2008; Pascault et al., 2010; Beyaert and Paul Voroney, 2011; Bray et al., 2012). Senescent leaves had a higher lignin content than the green leaves. The lignin content may, therefore, explain the difference in decomposition rate between the 2 types of litter. These results confirmed the general findings that the lignin content in *J. curcas* leaves reduced their decomposition rate (Trinsoutrot et al., 2000; Amougou et al., 2011). Arriaga and Maya (2007) and Allison (2012) reported that the chemical contents of mature residues and C:N ratio were negatively correlated with the decomposition rate as they reduced the degradation rates by decomposer microorganisms (Wardle et al., 2006; Esperschütz et al., 2013).

Nitrogen mineralization

It was found that the litter N content explained the changes in NH_4^+ mineralization during the early stage of incubation. The ammonification rate was higher for soils mulched with litter with a high N content. Previous studies on letter have reported a positive correlation between N mineralization rates and N content (Banning et al., 2008; Abbasi et al., 2014; Chaudhary et al., 2014). The initial lignin content in the litter explains the ammonification rates in the later stage of incubation. In this study, the net N mineralization pattern was similar to the nitrification pattern, as reported in other studies (Azeez and Van Averbeke, 2010). The similarity between the net N mineralization and nitrification rates suggested that ammonification was not only transitory in N transformation, but that the net ammonification rate is very low and ammonium is rapidly transformed into nitrate (Azeez and Van Averbeke, 2010).

Bacterial activity and community structure

Plant species differ considerably in the quality of litter that they produce and the species is often a major determinant of the decomposer community structure (Parmelee et al., 1989; Badejo et al., 1999). Our results confirmed the general findings of previous studies that the CO_2 flux is high during the early stage of incubation of plant residues (Sall et al., 2003; Dossa et al., 2009; Cleveland et al., 2013). This high CO_2 flux suggests an increase in microbial activity during this period and

corresponds to the use, by r strategists, of directly available, easily degradable compounds released from litter material (Esperschütz et al., 2013). Thereafter, k strategists colonize the litter during the later stages of decomposition (De Angelis et al., 2013). The end of the incubation period was marked by a decrease in microbial activity and an increase in bacterial diversity (Shannon diversity) confirming the findings of Dilly et al. (2004). The slow decomposition rate during the later stages was due to the decomposition of recalcitrant compounds (lignin and cellulose) by the decomposer communities mainly present in these stages (Esperschütz et al., 2013). The positive correlation between C mineralization and changes in bacterial community structure agrees with the findings of Basiliko et al. (2013). Our study also showed that bacterial diversity was negatively correlated with the litter C:N ratio, as also reported by Ge et al. (2010). The changes in the bacterial community with time may be explained by the chemical changes in the litter during the decomposition process (Wardle et al., 2006; Bray et al., 2012). According to Pfeiffer et al. (2013), litter with a low C:N ratio and low lignin content has only a minor impact on the soil bacterial community. Therefore, in rapid decomposing litter, r strategists will take up available nutrients rapidly leading to a reduction in bacterial diversity. However, k strategists colonized slowly decomposing litter such as *J. curcas* litter leading to an increase in diversity.

Conclusion

The chemical composition of the *J. curcas* litter depended on the geographical origin of the cultivars. There were correlations between the chemical composition of the litter, the decomposition rates and the bacterial community structures. The results showed that the double exponential decomposition model accurately predicted the changes in C content in *J. curcas* mulch. This mulch modifies C and N cycling and appears to have an effect on soil C sequestration.

Conflict of Interests

The authors declare that there is no conflict of interests.

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