Tropical Ecology **55**(2): 207-220, 2014 ISSN 0564-3295

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Decomposition and changes in chemical composition of leaf litter of five dominant tree species in a West African tropical forest

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Abstract: The objective of the research was to study the rate of decomposition and changes in the chemical characteristics in the leaf litter of selected tree species using a litterbag experiment. The decomposition of leaf litter from five dominant tree species, *Afzelia africana*, *Anogeissus leiocarpa*, *Ceiba pentandra*, *Dialium guineense*, and *Diospyros mespiliformis* was studied in the Lama forest reserve, a tropical vertisol forest in Benin. Changes in litter mass and organic compounds, including acid-hydrolysable (AH), water-soluble (WS) and ethanol-soluble (ES) compounds and Klason lignin, were determined every 4 weeks over 6-months period. The carbon (C), nitrogen (N), organic matter (OM) and ash contents of fresh litter were also determined. The high differences in the initial litter quality across the species resulted in a large variation of the absolute decay rate (k_a values), ranging from 1.69 to 4.67 year^{-1}. The key chemical controls of leaf decomposition were the initial concentrations of AH, lignin and N. The specific decay rates (k_s values) of AH, WS, ES and Klason lignin varied significantly within and across species and described leaf litter as composed of labile and recalcitrant C pools having different decay patterns. WS and ES had the highest k_s values of 4.65 to 11.96 year^{-1} and 4.06 to 21.27 year^{-1}, respectively, whereas AH had k_s values of 1.14 to 4.74 year^{-1} and seemed to impose its decay pattern on the whole litter. The results supported the hypothesis that litter chemistry was the main factor controlling the decomposition process at a local scale.

Resumen: El objetivo fue estudiar la tasa de descomposición y los cambios en las características químicas del mantillo foliar de especiesarbóreascon un experimento de bolsas de mantillo.Se estudió la descomposición del mantillo foliar de cinco especies arbóreas dominantes, *Afzelia africana, Anogeissus leiocarpa, Ceiba pentandra, Dialium guineense* y *Diospyros mespiliformis*, en la reserva forestal Lama, un bosque tropical de vertisol en Benín. Los cambios en la masa del mantillo y los compuestos orgánicos, incluyendo compuestos ácido-hidrolisables (AH), solubles en agua (SA) y solubles en etanol (SE),y la lignina Klason, fueron determinados cada cuatro semanas durante un periodo de seis meses. También se determinó el carbono (C), el nitrógeno (N), la materiaorgánica (OM) y el contenido de ceniza en el mantillo fresco. Las grandes diferencias en la calidad inicial del mantillo entre especies provocaronuna gran variación de las tasas absolutas de decaimiento (valores de k_a), de 1.69 a 4.67 año^{-1}. Los controles químicos clave de la descomposición foliar fueronlas concentraciones inicialesde AH,

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ligninay N. Las tasas específicas de decaimiento (valores k_s) de AH, SA y lignina Klason variaron significativamente al interior de las especies y entre ellas,y permitieron describir al mantillo foliar como una mezcla de contenidos de C lábil y recalcitrantecon patrones diferentes de decaimiento. SA y SE tuvieron sus mayores valores de $k_s$de 4.65 a 11.96 año^{-1}, y de 4.06 a 21.27 año^{-1}, respectivamente. AH tuvovalores de $k_s$de 1.14 a 4.74 año^{-1} y pareció imponer su patrón de decaimiento en todo el mantillo. Los resultados apoyanla hipótesis de que la química del mantillo fue el principal factor controlador del proceso de descomposicióna escala local.

Resumo: O objetivo do trabalho foi estudar a taxa de decomposição e alterações nas características químicas de espécies arbóreas selecionadas usando um dispositivo de serapilheira. A decomposição da folhada de cinco espécies de árvores dominantes, *Afzelia africana, Anogeissus leiocarpa, Ceiba pentandra, Dialium guineense*, e *Diospyros mespiliformis* foi estudada na reserva florestal de Lama, uma floresta tropical em vertisolos no Benin. As alterações na massa de folhada e de compostos orgânicos, incluindo os hidrolisáveisem ácido (AH), os compostos solúveis em água (WS) e os solúveis em etanol (ES) e a lenhina Klason, foram determinadas a cada 4 semanas durante o período de 6 meses. Os teores em carbono (C), o azoto (N), a matéria orgânica (MO) e as cinzas da folhada fresca foram também determinados. As grandes diferenças na qualidade inicial da folhada entre as espécies resultou numa grande variação da taxa absolutade decomposição (valores ka), variando entre 1,69-4,67 ano^{-1}. Os controles químicos chave da decomposição das folhas foram as concentrações iniciais de AH, lenhina e N. As taxasespecíficas de decomposição (valores ks) de AH, WS, ES e lenhinaKlason variaram significativamente dentro e entre espécies e descritas pelos stocks de C lábil e recalcitrante com diferentes padrões de decomposição. Os compostos WS e ES apresentaram os maiores valores de ks 4,65 a 11,96 ano^{-1} e 4,06 a21,27 ano^{-1}, respectivamente, enquanto os AH apresentaram valores ks de 1,14 a 4,74 ano^{-1} e parecia impor seu padrão de decomposição ao conjunto da folhada. Os resultados suportam a hipótese de que a química da folhada foi o principal fator a controlar o processo de decomposição à escala local.

Key words: Decay rate, litter quality, litterbag experiment, tropical forest.

Introduction

Litter decomposition after litter fall is a key process in the carbon (C) and nutrient cycling in terrestrial ecosystems. As climatic conditions drive the rate of litter decomposition at a global scale, litter decomposition is very fast in humid tropical forests and has a remarkable influence on the annual variability of C fluxes (Aerts 1997; Meentemeyer 1978). Although tropical forests are a critical component of the global C cycle (Pan *et al.* 2011), the driving factors of litter decomposition have been studied less thoroughly in the tropics than in other climatic regions.

Litter quality is the most important determinant of decomposition rates at a regional scale (Aerts 1997). Several studies have confirmed that decomposition in boreal as well as in tropical ecosystems is affected by the initial nitrogen (N) and phosphorus (P) concentrations and the C/N ratio of litter (e.g., Aerts 1997; Berg & Staaf 1980; Cleveland *et al.* 2006; Kaspari *et al.* 2008; Tian *et al.* 1992). In addition, the concentrations of tannins and polyphenolics are found to be related to decomposition activity (McClaugherty & Berg 1987; Ryan *et al.* 1990).

By analysing the effect of climate and litter chemistry, Meentemeyer (1978) showed that litter decomposition in terrestrial ecosystems was strongly controlled by actual evapotranspiration (AET) and lignin concentration. Several other studies conducted in boreal to tropical ecosystems indicated that the lignin/N ratio, the (lignin+cellulose)/N ratio or the (lignin+phenol)/N ratio can account for the variations in litter decomposition (e.g., Aerts 1997; Goma-Tchimbakala & Bernhard-Reversat 2006; Loranger *et al.* 2002).

Given the plant species richness of tropical forests and assuming chemically diverse litters (Barbhuiya *et al.* 2008; Cusack *et al.* 2009; Goma-Tchimbakala & Bernhard-Reversat 2006; Meng *et al.* 2011; Tynsong & Tiwari 2011), it is critical to

further investigate the effect of litter quality in the tropics in order to increase our ability to understand and predict the decomposition process in such environments. Decomposition studies conducted in Africa through litterbag experiments (Attignon *et al.* 2004; Bernhard-Reversat 1982; 1993; Bernhard-Reversat & Schwartz 1997; Bernhard-Reversat *et al.* 2001; Goma-Tchimbakala & Bernhard-Reversat 2006; Musvoto *et al.* 2000; Songwe *et al.* 1988) have reported data on C, N, P, mass loss and decay rate. Although further information on the changes in the concentration of sugars, waxes, celluloses, hemicelluloses and lignin in decomposing litter could shed more light on the litter decomposition process in tropical forests, these more specific analyses of the chemical composition of decomposing organic matter (OM) are currently missing.

The present study is among the first attempts to investigate the decomposition rate of different organic compounds of leaf litter in West Africa. The analyses on acid-hydrolysable (AH), water-soluble (WS) and ethanol-soluble (ES) compounds and Klason lignin add significantly to our understanding of litter decomposition in tropical forests on vertisols. This study provides data on the specific decay rate of AH, WS, ES and lignin and assesses how the litter quality influences decomposition in this particular ecosystem. Moreover, it provides important input, from a region where little is known about litter decomposition, into sophisticated dynamic soil C models (Chertov *et al.* 2001; Coleman & Jenkinson 1996; Currie & Aber 1997; Kurz & Apps 1999; Liski *et al.* 2005) used to study soil processes and the C cycle and to predict the global C balance. For example, Liski *et al.* (2005) and Tuomi *et al.* (2009) used, as a basis of dynamic soil C models, analyses on chemical composition of decomposing litter with a sequence of extractions (water-, ethanol- and acid-extractable compounds) studied by Berg *et al.* (1993).

Our objective was to study the rate of decomposition and changes in the chemical characteristics in the leaf litter of different tree species using a litterbag experiment. We studied five tree species, *Afzelia africana* Sm. (Caesalpiniaceae), *Anogeissus leiocarpa* (DC.) Guill. & Perr. (Combretaceae), *Ceiba pentandra* (L.) Gaertn. (Bombacaceae), *Dialium guineense* Willd. (Caesalpiniaceae) and *Diospyros mespiliformis* Hochst. Ex A. DC. (Ebenaceae), in the Lama forest, a moist tropical forest in West Africa. In addition to mass loss and proportions of organic compounds (AH, WS, ES and Klason lignin), we determined the C, N and ash content of litter of the studied species. Our study intended to test the hypothesis that differences in initial litter quality among the five species drive differences in decomposition rates at a local scale.

Material and methods

Experimental site and species selection

The study area is the Lama forest, a semi-deciduous forest located in a humid tropical climate in Southern Benin (Nagel *et al.* 2004) at 6°55' - 7°00'N, 2°04' - 2°12'E (Fig. 1). It has had the status of protected forest since December 1946, covering an area of 16,250 ha of which 3,784 ha is comprised of an entirely protected (reserved) natural dense forest area called "Noyau Central" (von Bothmer *et al.* 1986). The study site was located in this entirely protected part of the Lama forest.

The site falls within the tropical moist zone according to the classification scheme for climate regions of the IPCC (IPCC 2006, chapter 3 of 2006 IPCC Guidelines for National Greenhouse Gas Inventories). The highest (38 °C) and the lowest (15 °C) temperatures were usually recorded in February-March and in December, respectively. The mean annual temperature is 27 °C. The climate is characterized by a bimodal precipitation distribution. The mean annual precipitation in the study area is 1100 mm. In general, rainfall is more than 100 mm month^{-1} throughout the year, except in January, February and December. Years are divided into four seasons: two rainy and two dry seasons. The principal rainy season occurs between mid-March and mid-July and the shorter rainy season between mid-September and mid-November. The monthly average of relative humidity is always more than 51 %. The ranges of monthly climatic data recorded by the national meteorological service at the time of the decomposition experiment were as follows: temperature: 26.6 °C - 31.4 °C; precipitation: 80.1 mm - 192.4 mm; and evapotranspiration: 100.9 mm - 122.7 mm (Table 1).

According to the description reported by Küppers *et al.* (1998), the soil of the Lama forest consists of hydromorphic clayey vertisol (40 to 60 % of clay), having a poor drainage and a pH range of 5 - 5.5 in the 0 - 30 cm horizon. Its pH increases up to 6.5 - 7 in deeper horizons due to the appearance of limestone at a depth of 150 cm. The horizons at 0 - 10 cm and 10 - 30 cm were reported as 7.5 YR 2.5/1 and 7.5 YR 3/1 according to the

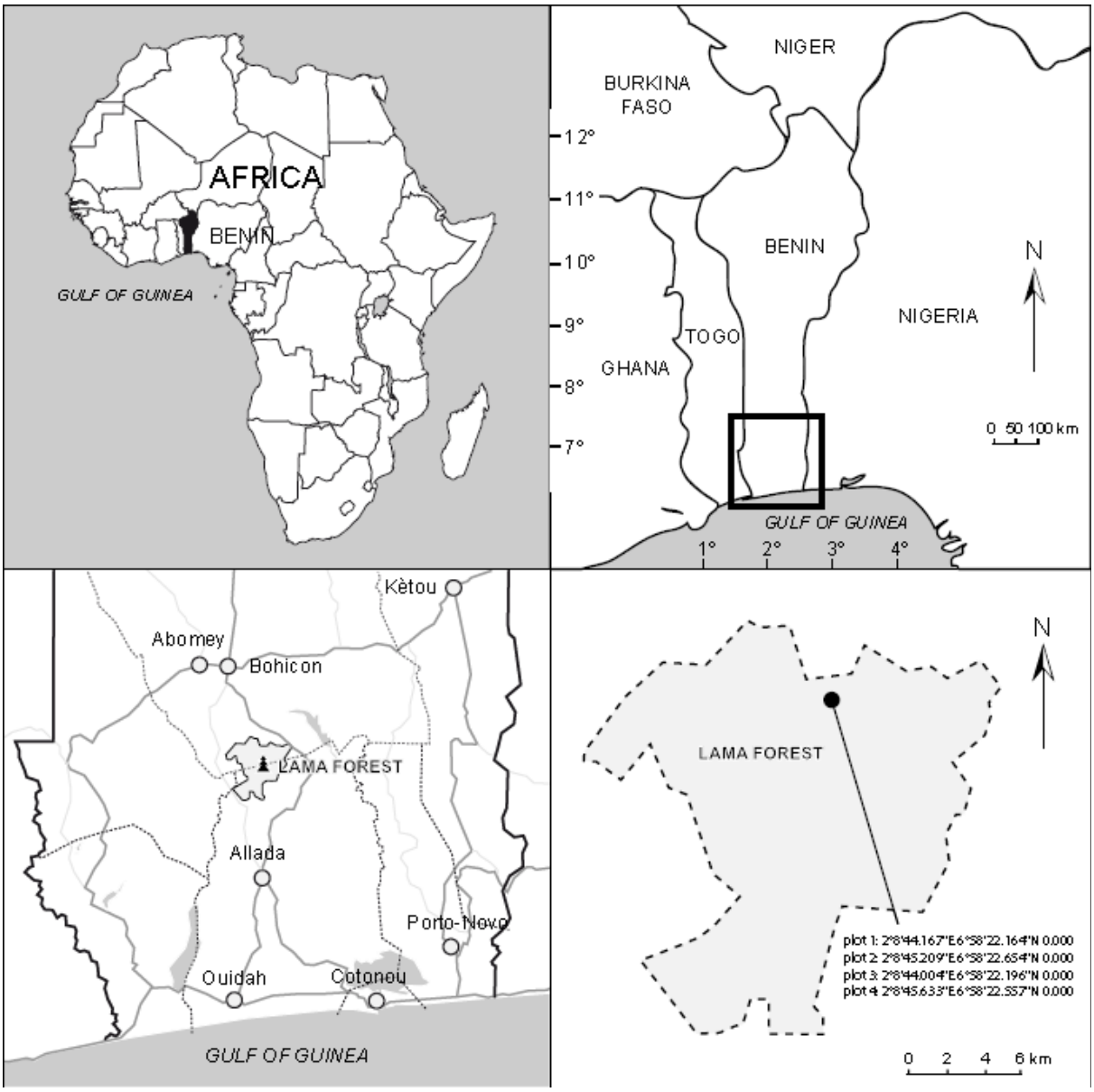

Fig. 1. Location of the study area in Benin.

Munsell universal soil colours chart. The Lama forest soil has been described as rich in calcium (Ca) and magnesium (Mg), which is due to a "granito-gneissic" parent material from the secondary and tertiary ages, and reported as a rare vertisol in West Africa. The mean altitude in the forest is 60 m (von Bothmer *et al*. 1986).

The tree species richness of the Lama plant communities was described by Akoègninou (1984), Mondjannagni (1969), Paradis & Houngnon (1977). Küppers *et al.* (1998) reported 67 families based on an inventory carried out in 1998. The average density in the "Noyau Central" is 12 species/400 m², and the relative abundance of dominant tree species is about 40 trees/400 m² (Küppers *et al.* 1998). The current research focused on five dominant tree species, namely the indigenous tree species *A. africana*, *A. leiocarpa*, *C. pentandra*, *D. guineense* and *D. mespiliformis* (Küppers *et al.* 1998; Nagel *et al.* 2004; von Bothmer *et al.* 1986). The diameter at breast height is up to 95 cm for *A. africana*, 89 cm for *A. leiocarpa*, 190 cm for *C. pentandra*, 56 cm for *D. guineense* and 53 cm for *D. mespiliformis* (Guendehou *et al.* 2012). No harvesting and fertilization activities are implemented in the forest where the study site was

Table 1. Monthly climatic data recorded during the litterbag experiment in 2010 by the meteorological stations Bohicon (temperature and evapotranspiration) and Toffo (precipitation) closest to the Lama forest. Evapotranspiration was calculated according to the equation of Penman.

Month	Temperature (°C)	Precipitation (mm)	Evapotranspiration (mm)
February	31.4	80.1	122.2
March	30.6	192.4	108.1
April	30.2	100.3	122.7
May	29	157.1	116.4
June	28.1	90.1	101.5
July	26.6	149	100.9

located. In the Lama forest, the amount of leaf litter fall ranges from 26 to 42 t dry matter year^{-1}; the litter fall follows a unimodal distribution pattern, with the maximum litter production observed during the dry season, often in January (Djego 2006).

Leaf litter collection

Leaf litter samples were collected in January 2010 in the "Noyau Central" area where the decomposition study was carried out. Only senescent leaves ready to fall from trees were collected, either by hand or using sticks. Leaves were collected separately by species from a variety of individuals by walking in "Noyau Central". Leaves of the same species were mixed. Leaf litter on the floor was considered partly decomposed and chemically different from fresh litter and, therefore, not applicable to this study. The leaf litter used to determine the initial litter quality and that used in the decomposition study were collected at the same time. The leaves collected were dried in open-air (ambient temperatures) and then oven-dried at 75 °C to constant weight. An assumption was made that drying leaves at this moderate temperature would minimize the loss of material, in particular, of volatile organic compounds, likely to occur at higher temperatures.

Litterbag preparation

The litterbag used was made of polyester net fine mesh (0.33 mm). The mesh size was assumed small enough to limit the physical loss of fresh litter from the bag, to reduce the intervention of invertebrates and to allow aerobic micro-organism activity. It was smaller than in other studies (Attignon *et al.* 2004; Berg *et al.* 1993; Cusack *et al.* 2009; Goma-Tchimbakala & Bernhard-Reversat 2006; Trofymow *et al.* 2002). In our experiment, decomposition was assumed mainly microbial (Prescott 2005; Stewart & Davies 1989). By using litterbags that reduce the intervention of invertebrates, we assumed that the decay rates resulting from microbial decomposition were not underestimated. The litterbag in this study was a square 20 × 20 cm bag. Leaves of each studied tree species were incubated individually. Based on the amount of litter collected, a 20 g dry weight of *A. africana*, 30 g of *A. leiocarpa*, 20 g of *C. pentandra*, 30 g of *D. guineense* and 30 g of *D. mespiliformis* was initially placed in the bags. There were in total 24 bags for each litter type for the whole experiment. Dried litter samples were carefully filled in the bags, and precautions were taken to avoid leaf litter from crushing or breaking into small pieces. The bag was then sewed with a polyester string.

Litterbag exposure in the field

Litterbags were divided between four plots established in a nearly rectangular configuration. The distance between the plots was between 25 and 30 m. This distance was assumed large enough to minimize the spatial autocorrelation between the plots. Four plots (four replicates) were used in order to assess the variations in the decomposition process. In each plot, a total of 30 litterbags were placed in rows and columns on the forest ground: there were five columns, each containing different litter types, and six rows, each containing the samples to be collected at the same time. In each row, the five bags representing different litter types were placed randomly. Litterbags were left on the ground in the "Noyau Central" area of the Lama forest on February 5, 2010 and were not moved until the collection date. In two plots, a wire mesh fence was placed to protect from possible disturbances by animals. However, during the incubation period none of the plot was disturbed.

Litterbag collection and mass loss measurement

Litterbags were collected every 4 weeks. In each plot, the first row was collected at 4 weeks, the second row at 8 weeks and so on until the last row at 24 weeks. Only samples ready to be collected were collected, and other samples were not moved to avoid disrupting the decomposition

process. The collected bags were carefully brushed out and cleared of foreign material (soil, roots and fauna), and the remaining litter in the bag was dried in open-air and then oven-dried at 75 °C to constant weight before being weighed to determine the mass loss. Since the chemical analyses were not done on the same day after the mass loss measurement, the remaining litter was kept in a freezer in a plastic bag.

Chemical analyses for determining litter quality

The litter quality prior to decomposition and the chemical composition of decomposed litter over time were determined in the laboratory of the Finnish Forest Research Institute. Litter samples were homogenously milled. Thereafter, samples were analysed for ethanol-soluble compounds (e.g., waxes), water-soluble compounds (e.g., sugars, phenolics), acid-hydrolysable compounds (polymer carbohydrates, e.g., celluloses, hemicelluloses) and compounds neither soluble nor hydrolysable (Klason lignin, other aromatic compounds) which constitute the essential carbonaceous constituents of leaf litter. Extraction was conducted in a sonicating water bath, first for 90 min with ethanol, then for 90 min with water (Karhu *et al.* 2010). The ethanol and water extracted residue was divided into acid-hydrolysable (72 % H_2SO_4) and non-hydrolysable fractions using the Klason lignin method (Effland 1977). Samples were filtered, oven-dried at 75 °C to constant weight and weighed between the extractions, and the amounts of different fractions were determined as the mass of OM. The ash content of the samples was determined after keeping the dried samples in a muffle furnace at 550 °C overnight. As ash does not decompose during the litterbag experiment, not taking it into account will result in an underestimation of mass loss and chemical fractions (when reported with regard to initial litter mass). Therefore, all masses reported in this study were expressed as ash free, i.e. only OM was considered.

OM, C and N concentrations of the litter prior to decomposition were also determined. The total C and N content was analysed with a Leco CHN device (Leco, St Joseph, MI) in the Central Laboratory of the Finnish Forest Research Institute, an accredited test laboratory (complying with the SFS-EN ISO/IEC17025 standard). Due to high number of analyses associated with each collection (160 chemical parameters to be measured), samples from the same litter and same collection were pooled for chemical analyses in order to reduce the amount of work. This approach was assumed to yield the average chemical composition of the four plots.

Data analysis

Single negative exponential decay model (Olson 1963) widely applied in decomposition studies (e.g., Aerts 1997; Gallardo & Merino 1993; Stewart & Davies 1989) was fitted to the observations on remaining mass in the five litter species studied using the statistical computing software R (R Development Core Team 2009) and the following Eq.(1):

$$M_t = M_0 \times e^{-kt} \quad (1)$$

where, k = decay rate, M_t = remaining mass at time t, M_0 = initial mass at t = 0. The models were evaluated based on standard error and the significance of k value, the coefficient of determination and the residual standard error of the model derived using the statistical computing software R. This enables to test that the model fits the data very well. Eq.(1) was also fitted to the remaining mass of AH, WS, ES and Klason lignin, which enabled determining the specific decay rate of each chemical fraction.

The five dependent observations on decay rates (k) were regressed against each of the ten litter chemical parameter, including the initial concentrations of AH, WS, ES, lignin and initial OM, C, N, ash content as well as the C/N, lignin/N ratios. Thus, we could determine which litter quality parameters affect decay rates. Regressions were assessed based on standard errors and the significance of regression parameters, the adjusted coefficient of determination (adj. R^2) and P values.

Results

Initial litter chemistry

AH was the most abundant chemical compound in the studied litters; its concentration ranged from 432 to 545 mg g^{-1} of initial OM, which is 2 to 6 times that of WS, ES and lignin (Table 2, Fig. 2). It was at its highest in *A. africana* which had the lowest C/N and lignin/N ratios (Table 2) and at its lowest in *D. mespiliformis*. The measured Klason lignin concentrations ranged from 110 to 223 mg g^{-1} of OM and were at their highest in *C. pentandra*, which had the lowest ash content, and at their lowest in *A. leiocarpa*. WS concentrations ranged from 138 mg g^{-1} in *D. guineense* to 282 mg g^{-1}

Table 2. Initial concentrations of acid-hydrolysable (AH), water-soluble (WS) and ethanol-soluble (ES) compounds and lignin in each studied leaf litter, in mg g^{-1} of organic matter of litter; initial carbon (C), nitrogen (N), ash content as percentage (%) of organic matter; initial organic matter (OM) as percentage of dry matter; and C/N and lignin/N ratios: mean ± standard error; CV: coefficient of variation (variation between species).

	Leaf litter species					CV (%)
	Afzelia africana	*Anogeissus leiocarpa*	*Ceiba pentandra*	*Dialium guineense*	*Diospyros mespiliformis*	
AH	544.9 ± 0.08	525.6 ± 0.02	541.0 ± 0.03	447.4 ± 0.03	431.7 ± 0.14	11
WS	203.4 ± 0.11	188.7 ± 0.05	147.8 ± 0.02	138.3 ± 0.03	281.7 ± 0.05	30
ES	113.4 ± 0.07	176.0 ± 0.03	88.4 ± 0.02	221.9 ± 0.03	153.3 ± 0.02	35
Lignin	138.3 ± 0.16	109.7 ± 0.03	222.8 ± 0.01	192.3 ±0.01	133.2 ± 0.14	29
OM	91.80 ± 0.55	89.50 ± 0.1	92.57 ± 0.18	88.63 ± 0.59	85.33 ± 0.29	3.2
C	49.53 ± 0.09	47.80 ± 0.06	50.13 ± 0.03	46.40 ± 0.10	47.63 ± 0.22	3.1
N	2.84 ± 0.10	1.85 ± 0.00	2.73 ± 0.03	1.93 ± 0.03	1.89 ± 0.05	22
C/N	17.47 ± 0.68	25.84 ± 0.03	18.37 ± 0.23	24.05 ± 0.38	25.20 ± 0.83	18
Lignin/N	4.87 ± 0.76	5.93 ± 0.18	8.16 ± 0.08	9.96 ± 0.21	7.05 ± 0.69	27
Ash	7.22 ± 0.003	9.00 ± 0.006	6.68 ± 0.002	11.02 ± 0.006	13.58 ± 0.005	30

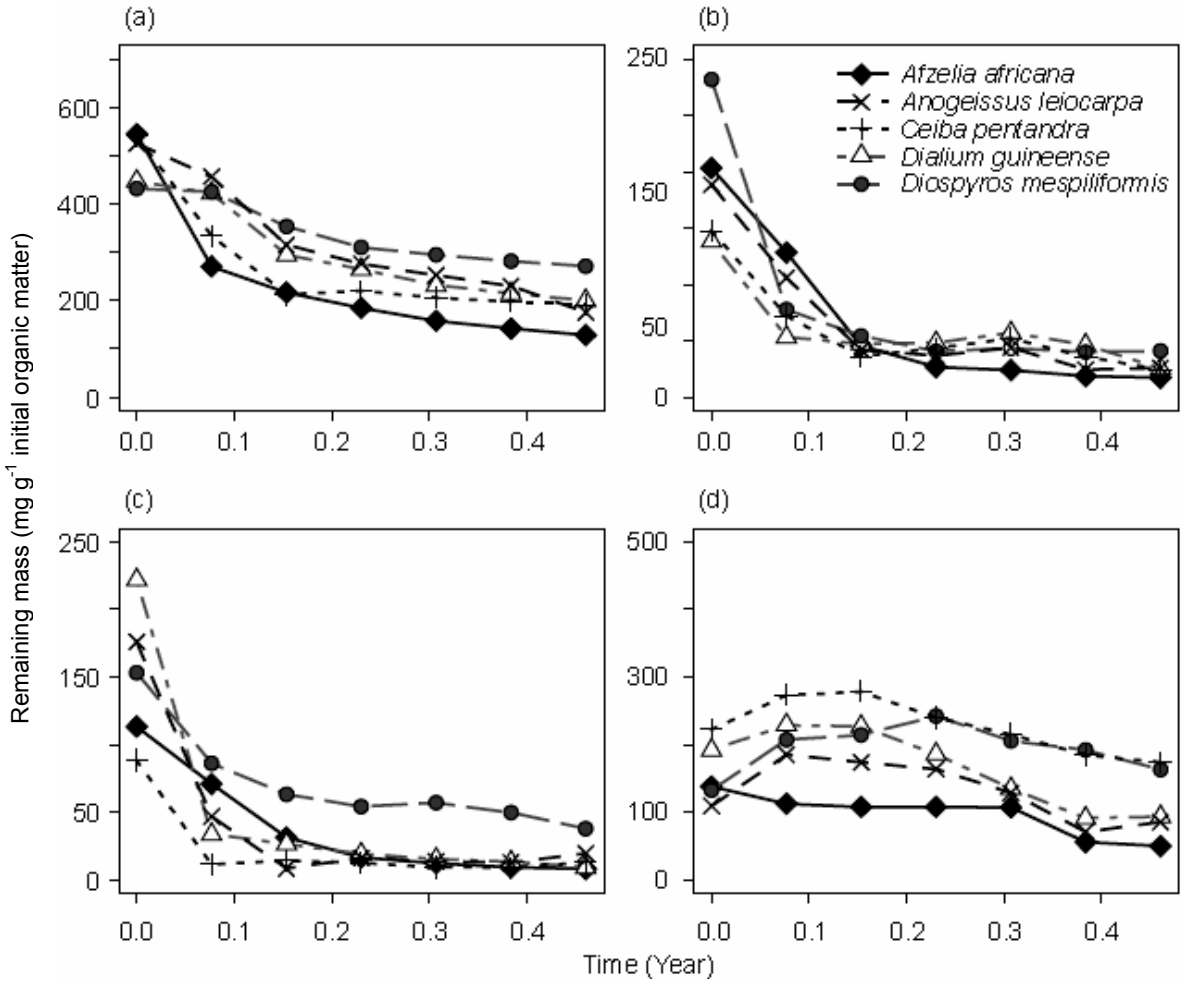

Fig. 2. Remaining mass (mg g^{-1} initial organic matter) of acid-hydrolysable compounds (a), water-soluble compounds (b), ethanol-soluble compounds (c) and lignin (d) measured every 4 weeks during the decomposition of the leaf litter of each species.

Table 3. Absolute decay rate of leaf litter of each studied species (k_a values ± standard error) derived from the single exponential decay model fitted to data on litter mass loss; specific decay rate (k_s values ± standard error) of each chemical compounds group in studied leaf litters, derived from the single exponential decay model fitted to the data on mass loss of each compound group. Significant k_a and k_s values are indicated with ***$P < 0.001$, **$P < 0.01$ *$P < 0.05$, and not significant with ns. Figures in brackets are R^2.

Species	k_a values (year^{-1})	k_s values (year^{-1})			
		Acid-hydrolysable	Water-soluble	Ethanol-soluble	Lignin
Afzelia africana	4.67 ± 0.25*** (0.91)	4.74 ± 0.69*** (0.83)	7.68 ± 0.68*** (0.86)	7.37 ± 0.43*** (0.93)	1.68 ± 0.27*** (0.75)
Anogeissus leiocarpa	2.93 ± 0.12*** (0.90)	2.47 ± 0.15*** (0.95)	6.98 ± 0.87*** (0.78)	16.75 ± 2.79*** (0.31)	-0.12 ± 0.60 (ns) (0.26)
Ceiba pentandra	2.59 ± 0.15*** (0.84)	3.53 ± 0.56*** (0.66)	5.61 ± 1.06** (0.66)	21.24 ± 7.17* (0.30)	0.19 ± 0.25 (ns) (0.50)
Dialium guineense	2.78 ± 0.08*** (0.97)	2.00 ± 0.15*** (0.92)	4.65 ± 1.06** (0.56)	21.28 ± 3.99** (0.73)	1.03 ± 0.42* (0.74)
Diospyros mespiliformis	1.69 ± 0.07*** (0.92)	1.14 ± 0.08*** (0.92)	11.96 ± 2.65** (0.56)	4.06 ± 0.58*** (0.81)	-1.07 ± 0.35* (-0.17)

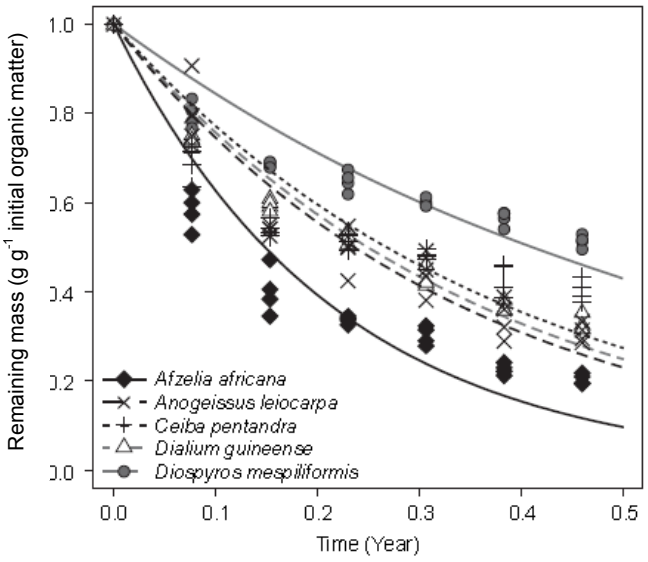

Fig. 3. Remaining mass of organic matter (g g^{-1} initial organic matter) of decomposing litter of each species measured every 4 weeks from the four plots over a 6-months period (dots) and the single exponential decay model fitted to the observations (lines).

in *D. mespiliformis,* while ES concentrations varied from 88 mg g^{-1} in *C. pentandra* to 222 mg g^{-1} in *D. guineense*. The variation in chemical fractions across species was higher in WS (30 %), ES (35 %) and lignin (29 %) than in AH (11 %) (Table 2).

The highest N concentrations of initial leaf litter were measured for *A. africana* (2.8 % of OM) and *C. pentandra* (2.7 % of OM) respectively. The N concentrations of descending leaves of the other three studied tree species, *A. leiocarpa*, *D. guineense*, and *D. mespiliformis*, were less than 2 %. The observed interspecies variations in N concentration and C/N ratio were 22 % and 18 %, respectively.

The initial OM and C content was higher in *A. africana* and *C. pentandra*; however, not subject to large variation between species. The initial ash content was at its highest in *D. mespiliformis*, ranging from 6.7 to 13.6 % of dry matter and varying across species (Table 2).

Litter decay rates and changes in litter chemistry

The exponential decay model fits to the data very well (high R^2 and model parameters significant) (Table 3). *A. Africana* had the highest decay rate (k_a values), followed by *A. leiocarpa*, *D. guineense*, *C. pentandra* and *D. mespiliformis* (Table 3). There was large variation in k_a values across species (coefficient of variation 37 %). The variation of k_a was not strongly related to any of the measured chemical properties of the tested litter types based on the analysis of the regressions.

Within a species, each chemical fraction (AH, WS, ES and lignin) decomposed according to its own decay rate (k specific, hereafter k_s values) (Table 3). k_s values varied significantly within and between species. The highest k_s values were identified in WS or ES (Table 3) followed by AH. The k_s values in AH were closest to the k_a values for each species.

In *A. africana*, WS and ES seemed to decompose in a similar way (close k_s values). In contrast to *A. leiocarpa*, *C. pentandra* and *D. guineense* in which ES decomposed faster than WS (the k_s values in ES were 2.4 to 4.6 times those of WS), WS had k_s values three times those of ES in *D. mespiliformis* (Table 3).

As decomposition progressed, the concentrations of AH, WS and ES decreased whereas the fraction of lignin increased (in general during the first eight weeks) before decreasing. The highest decreases in chemical fractions were observed across all species in AH (Fig. 2). The litter decomposition was faster during the first 8 weeks, and the order of magnitude of mass losses observed at this stage was *A. africana* > *C. pentandra* > *D. guineense* > *D. mespiliformis* > *A. leiocarpa*. After this stage, the concentrations of WS and ES seemed to stabilise to a certain low level (1.7 to 4.1 % of initial OM for WS and 0.8 to 3.7 % for ES), whereas the fractions of AH remained higher (13 to 27.1 % of initial OM).

Fig. 3 shows that there were no large differences in remaining mass between plots. As composite samples were used in the chemical analyses, the variation in the litter chemistry of decomposed litter across plots was not assessed.

Discussion

Initial litter chemistry

The initial chemical compositions varied largely across the studied leaf litters, especially in terms of soluble compounds and Klason lignin. Celluloses and hemicelluloses measured as acid-hydrolysable compounds (AH) were the dominant organic compounds in descending leaves and varied less across species than other measured organic fractions. AH fractions also showed the highest loss during the decomposition of leaf litter, and this pattern was similar among species. The observed large interspecies variation in the initial chemical fractions agreed with earlier studies conducted in India, South America and Africa (Barbhuiya *et al.* 2008; Cusack *et al.* 2009; and Goma-Tchimbakala & Bernhard-Reversat 2006). However, these earlier studies reported even larger variability in the chemical composition between tree species than this study. All initial chemical fractions reported by Cusack *et al.* (2009), except for lignin, were 28 to 58 % lower than our data, and the lower initial N they found resulted in higher C/N and lignin/N ratios in their litters. Barbhuiya *et al.* (2008) reported initial cellulose + hemicelluloses concentrations that were 35 % lower than AH in our study and lignin concentrations that were 25 % higher. The initial fractions of cellulose + hemicelluloses and non-phenolic soluble + soluble phenolics reported by Goma-Tchimbakala & Bernhard-Reversat (2006), the only study to our knowledge having investigated the chemical fractions of leaf litter in Africa, were largely lower (44 to 47 %) than the average in our study. These discrepancies may be explained by differences in the studied tree species, methods, and environmental factors such as climate, soil type (e.g., our experiment was implemented on vertisol, whereas other studies were conducted on sandy clay loam or sandy clayey). However, these discrepancies support the finding that leaves of tropical species are chemically very diverse. Furthermore, Goma-Tchimbakala & Bernhard-Reversat (2006) did not consider litter ash content which is relatively high in tropical leaves (Reddy & Elanchezhian 2008; Singh & Mudgal 2000).

The C content in *A. africana* and *C. pentandra* was consistent with those reported by Weibel (2003) in the Lama forest. For all species, apart from *D. guineense*, the C content was slightly higher than the default value (47 %) proposed by IPCC (2006), suggesting that the use of the IPCC data would underestimate the C content by up to 6.2 %. In contrast to C content, the N content in *A. africana* and *C. pentandra*, reported by Weibel (2003) and that in *C. pentandra*, determined by Songwe *et al.* (1995), was largely lower (37-62 %) than in our study. An explanation of these differences may be that these studies did not consider the ash content in leaf litter, leading to a lower N content. If all data was reported with ash content, our results would be consistent with the other studies. Also, the N content in Goma-Tchimbakala & Bernhard-Reversat (2006) was 32 % lower than in our study; however, in addition to ash content, the material they used was mixed leaf litters of species different from those in our study. In our study, however, the N content was consistent with the range reported by Aerts (1997) for leaf litter in tropical regions. The lignin concentration reported in this study was consistent with that reported by Aerts (1997). The C/N ratios, even though lower than those determined by Weibel (2003), support the fact, also reported by Weibel (2003), that the C/N ratio in *A. africana* was lower than in *C. pentandra*. The C/N and lignin/N ratios were slightly higher than the lower limits of the wide ranges reported by Aerts (1997).

Ash content was a chemical parameter often absent from studies (such as Attignon *et al*. 2004; Bernhard-Reversat & Schwartz 1997; Goma-Tchimbakala & Bernhard-Reversat 2006; Songwe *et al*. 1995) on leaf litter decomposition in Africa. Han *et al*. (2012) and Singh & Mudgal (2000) reported ash content values of 12.25 % and 2.2 to 24 % for tropical leaves in China and India, respectively. In future decomposition studies of tropical tree species, taking ash content into account would improve the accuracy of the decomposition data.

Litter decay rates and changes in litter chemistry

The large variation in fresh litter quality driven by WS, ES, lignin and N was reflected by the 37 % variation in k_a values. Barbhuiya *et al*. (2008) and Cusack *et al*. (2009) reported a variation of 46 % and 49 %, respectively, in the decay rates of leaf litters of initial chemical fractions showing variation ranges of 19 - 40 % (Barbhuiya *et al*. 2008) and 28 - 45 % (Cusack *et al*. 2009). Scott & Binkley (1997) also found that initial litter chemistry affects litter decay rates. Even if temperature and precipitation are important factors that influence since the decomposition process in the tropics, is highly dynamic, dynamic approach (dynamic soil modelling) may by needed to explain variation in it. Since our experiment was conducted on a single site, these factors were not considered. In our study, the edapho-climatic conditions were identical for all studied litter types, and the differences in decomposition across species were due to quality of litter. It is widely reported that differences in decomposition rates between litter types are driven by litter chemical composition at a local scale (Aerts 1997; Berg *et al*. 1993; Lavelle *et al*. 1993; Loranger *et al*. 2002). The importance of litter quality is clearly illustrated by a review of Aerts (1997) who found that litter chemistry parameters are the best predictors of decay rates, especially in the tropics. According to Aerts (1997) the best predictor was the lignin/N ratio explaining 57 % of the variance in decay rates, whereas in our study on vertisol, the decay rates cannot be explained by any of the measured variables. Since the decomposition process in tropics is highly dynamic, dynamic approach (dynamic soil modelling) may be needed to explain variation in it.

k_a values represent litter that decomposes as a uniform C pool, whereas k_s values describe litter that has a labile, rapidly decomposing C pool and a slowly decomposing C pool. The observed high variation in k_s values within species, in particular higher k_s values in WS and ES, accounted for the rapid decomposition of labile C contained in WS and ES. The high differences in k_s values between species (e.g., k_s values in WS were higher in *D. mespiliformis* than in other species and k_s values in ES were higher than in *A. leiocarpa*, *C. pentandra* and *D. guineense*) explained the species control over the initial litter chemistry. This leads to the conclusion that chemical fractions decomposed according to species. The preference of microorganisms to decompose certain chemical fractions originating from a certain species rather than from other species may have contributed to these differences in k_s values.

As AH was dominant in the leaf litter studied, varied little across species and was subject to the highest mass loss, in contrast to WS and ES, it seemed to impose its k_s values on the whole litter of all species (the k_s values in AH were closest to the k_a values) (Table 3).

As decomposition progressed, the quality of litter varied continuously (Fig. 3) with the effect of chemical fractions also changing. The order of magnitude of mass losses observed during the first 8 weeks correlated with the corresponding order of magnitude of the initial N content and inversely with the order of magnitude of the C/N ratios. This indicates that the higher the N content in fresh litter the higher the mass loss at early stages of decomposition. This observation was also consistent with other studies (Berg & Staaf 1980; Berg *et al*. 1987; Berg & Ekbohm 1991; Berg *et al*. 1996) which reported that mass loss at an early stage may be related to the concentrations of the major nutrients, such as N, P and sulphur (S), not only within a single species but also over several species. After 8 weeks, litter chemistry was dominated by AH, lignin and N, thus driving the decomposition process in subsequent stages. A possible explanation of the effect of AH, lignin and N on the decomposition process (k_a values), mainly after the stabilisation of WS and ES to a rather low level following the rapid decomposition at early stages, may be that lignin forms more recalcitrant compounds with N and that products of lignin degradation react with N (ammonia or amino acids) to form recalcitrant complexes (Nömmik & Vahtras 1982). Thus, the remaining AH would be shielded by lignin (Berg 2000) and these recalcitrant complexes. In addition, high N concentrations may block the degrading enzyme

system of decomposing organisms (Keyser *et al.* 1978), and, because of its high concentration observed during the decomposition process, AH would form stable complexes in the soil.

The decomposition of AH, WS, ES and lignin in Benin was faster than expected based on the data on leaf litter, fine root and climate analysed by Tuomi *et al.* (2009). In the dataset used by Tuomi *et al.* (2009), however, there was only data from five sites in the tropics in Central America, indicating that the dataset did not incorporate the large diversity of litter quality and the full cycle of litter decomposition in the tropics.

k_a values (Table 3) were consistent with those reported by Attignon *et al.* (2004) for *A. africana* and *C. pentandra* in the Lama forest. All k_a values, except in *D. mespiliformis*, were higher than those reported by Goma-Tchimbakala & Bernhard-Reversat (2006) for mixed leaf litter in a tropical forest in Congo. Only the k_a values of *A. africana* were outside the range reported by Muoghalu *et al.* (1994) for deciduous trees in a secondary rainforest in Nigeria. Cusack *et al.* (2009) reported k_a values that were lower than in our study, whereas Barbhuiya *et al.* (2008) reported a wide range of values. There are probably several reasons for the differences in k_a values obtained in various studies. Besides litter quality, other factors such as soil type, climate and decomposing organisms may have contributed to these differences.

Changes in litter chemistry are likely to occur as a result of changes in plant productivity and plant species composition due to climate change (Aerts 1993; Farooqui & Sekhar 2011; Melillo *et al.* 1993; Parsons *et al.* 1994, 1995). At the moment, however, the available scientific knowledge does not allow us to accurately quantify this effect and its influences on k_a values at a local scale.

Conclusions

This study provided data on the differences in litter quality, the decay rates of litter as a whole and the specific decay rates of chemical fractions for the leaf litter of five tree species in a tropical forest. The key chemical controls of leaf litter decay included acid-hydrolysable compounds, Klason lignin and nitrogen. Our results have important implications for predicting leaf litter decay in this particular ecosystem, but there are also align with well established ecological theory. The study provides evidence that litter quality controls the decomposition at a local scale and that litter is composed of labile and recalcitrant C pools having different decay patterns. It provides inputs to dynamic soil C models used to study the global C cycle and increases our ability to estimate the contribution of decomposition process in Africa to the global C balance. In our view, future studies should investigate litters from other tree species existing in Africa.

Acknowledgements

This work was supported by a scholarship from "Commission Nationale d'Attribution de Bourses de Stages du Bénin" (National Committee of Scholarship of Benin). We would like to thank "Conseil Scientifique de l'Université d'Abomey Calavi du Bénin", "Office National du Bois du Bénin", Dr. Riitta Pipatti at Statistics Finland and Professors Jari Varjo and Pasi Puttonen at the Finnish Forest Research Institute. We also thank two anonymous reviewers for their useful comments on this manuscript.

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(Received on 26.07.2012 and accepted after revisions, on 06.01.2013)