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Changes in relationships between initial litter quality and CO_2 release during early laboratory decomposition of tropical leaf litters

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Abstract – The relationships between initial litter quality with respiration during the early stage of decomposition was investigated in the litters of different tropical species from natural and planted fallows, and from tree plantations. CO_2 release was measured at 1- to 6-d intervals during 21 d. No significant relationship was found between total CO_2 release and any initial compound content. The rate of respiration versus time showed two stages. During the first stage, CO_2 release rate was high and appeared to be negatively related to polyphenols, suggesting an inhibition. During the second stage, CO_2 release rate was lower and was positively related to water-soluble phenolics, and to the soluble C/soluble N ratio. Total nitrogen and lignin content did not exhibit any effect on the respiration rate at this stage. © Elsevier, Paris

Tropical trees / litter decomposition / CO_2 release / litter quality / phenolic compounds

Résumé – Changements dans les relations entre qualité de la litière et respiration pendant la phase initiale de décomposition in vitro de litières de feuilles tropicales. Les relations entre la qualité initiale de la litière et la respiration pendant les premiers stades de décomposition au laboratoire ont été étudiées sur les litières de quelques espèces tropicales venant de jachères naturelles, de jachères plantées et de plantations forestières. Le dégagement de CO_2 a été mesuré à des intervalles de 1 à 6 j pendant 21 j. Aucune relation n'a été observée entre la quantité totale de carbone respiré en 21 j et les paramètres mesurés. Le taux de respiration a montré deux phases. Pendant la première, le taux de dégagement de CO_2 était élevé et négativement corrélé avec la teneur initiale des litières en composés phénoliques insolubles à l'eau. Pendant la deuxième phase, le taux de dégagement de CO_2 était plus faible et était corrélé avec la teneur initiale en composés phénoliques solubles à l'eau, et avec le rapport C soluble/N soluble. Aucun effet des teneurs en lignine et en azote n'a été mis en évidence au stade étudié. © Elsevier, Paris

Arbres tropicaux / décomposition / respiration / qualité de la litière / composés phénoliques

1. INTRODUCTION

Relationships between litter decomposition and litter quality are extensively studied but they are, however, not yet clearly established [8, 26]. The effect of nitrogen content and biochemical compounds, such as lignin, cellulose and polyphenols, on decomposition rate are still in discussion. The influence of initial nitrogen content, C/N ratio, lignin and lignin/N was studied by numerous authors [5, 18, 23], while some authors point out the role of polyphenols [6, 22].

Whereas decomposition rate is generally measured by weight loss, it is also measured by carbon dioxide release in numerous studies [20, 24], and CO_2 release from litters is also used to study the influence of litter quality [27], external factors such as litter temperature and humidity or salt [19, 21, 30] and litter mixing [17]. This method is less commonly used because it needs experimental devices which are farther from the natural conditions needed for weight loss measurements. However, CO_2 measurements allow the study of shorter time lags and consequently to distinguish different stages in early decomposition process which cannot be stated with weight loss measurements. At the hour scale, they can be used in microbial kinetic studies [14].

The aim of the present study was to investigate the relationships between CO_2 release and initial chemical composition during the early stage of decomposition in the litter of different tropical species from natural fallows, planted fallows and tree plantations.

2. MATERIALS AND METHODS

2.1. Materials

Litters were collected in tree plantations or natural fallows of savannah regions with annual rainfall between 800 and 1 200 mm.

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Tree leaf litters from Senegal were collected from native trees in natural fallows and from two exotic trees from planted fallow and plantation [13]; herbaceous materials from a natural fallow and from planted *Andropogon gayanus* were also collected. Tree leaf litters from Cameroon were collected from native and exotic trees in planted fallows [12]. Litters from Congo were collected in tree plantations [4]. The list of species is given in *table I.*

Collections were carried out in order to get fresh litter. In Senegal, litters were collected on the soil after leaf fall during the dry season. In Congo, they were collected by picking out on the soil fresh leaves which were recognised by their colour. In Cameroon, they were collected weekly in quadrats. Herbaceous material was obtained by cutting grasses when dried in the dry season, and was assumed to be comparable with fresh litter.

2.2. Litter analysis

Chemical analyses were made on air-dried and milled litters and chemical contents were expressed against oven-dried (75 °C) weight. Nitrogen was analysed on 100-mg samples by a LECO FP 428 CHN apparatus. Fibres were analysed by the Van Soest method [29] as acid detergent fibre (ADF) and acid detergent lignin (ADL) at the same laboratory. This method includes a variety of compounds in the so-called 'lignin' fraction but is generally used for comparisons. Nitrogen and fibre analysis were performed at the Cirad analysis laboratories ('Centre de coopération international en recherches agronomiques pour le développement', Montpellier, France). Soluble C and soluble phenolics were extracted by mixing 2 g litter in 60 mL cold water during 2 h, and the same method was used with addition of 1 mL 0.1 N HCl for soluble N extraction. Total extractable phenolic compounds (thereafter called total phenolics) were extracted according to the TSBF method [1] by heating 0.5 g litter in 50 % methanol in water at 80 °C during 1 h; the difference between methanol extracted phenolics and water extracted phenolics is referred to as 'insoluble phenolics', and the phenolic compounds which are not extracted by methanol are not taken into account in this study. Soluble carbon was determined in water extracts by the chemical oxygen demand (COD) with the rapid HACH method [2]. For conversion of COD to carbon, the approximation was made that it consisted mainly of glucids. Phenolic compounds were determined in water extracts and in methanol extracts by the tyrosin reagent (HACH method, [2]) which takes into account all hydroxylated aromatic compounds. Soluble nitrogen was determined after mineralisation in concentrated sulphuric acid and neutralisation of the extract, either by the Nessler reactant or by the salycilate reactant, both using the HACH methods [2].

Leaf thickness was measured with a thickness gauge after rehumidification of whole or fragmented litter leaves in boiling water.

2.3. Carbon dioxide release measurements

The carbon dioxide measurement device was previously described [3]. Measurements were made during 21 d, with 5–6 g coarsely fragmented litter (1 to 2 cm wide and long fragments) laid on 50 g pure sand in a closed tube at 30 °C. The litter was inoculated with 2 mL soil extract, prepared with 20 g savannah soil from Senegal in 100 mL water, stirred for 15 min and settled in order to use the suspension of fine soil particles in water. At 1- to 6-d intervals, the accumulated CO_2 was collected by air circulation and bubbling in two successive washing bottles containing 0.1 to 0.5 N

Table I. Origin and species of studied litters.

Country and region	Rainfall ($mm \cdot yr^{-1}$)	Vegetation	Status	Origin	Phenology	Form
Senegal, Sine Saloum	800	Mixed fallow grasses	natural	native	deciduous	grass
Senegal, Sine Saloum	800	*Andropogon gayanus*	planted	native	deciduous	grass
Senegal, Sine Saloum	800	*Guiera senegalensis*	natural	native	deciduous	shrub
Senegal, Sine Saloum	800	*Combretum glutinosum*	natural	native	evergreen	tree
Senegal, Sine Saloum	800	*Pilostigma thoningii*	natural	native	evergreen	tree
Senegal, Casamance	1 040	Mixed fallow grasses	natural	native	deciduous	grass
Senegal, Casamance	1 040	*Terminalia macroptera*	natural	native	deciduous	tree
Senegal, Casamance	1 040	*C. geitonophyllum*	natural	native	evergreen	tree
Senegal, Casamance	1 040	*Acacia holosericea*	planted	exotic	evergreen	tree
Senegal, Casamance	1 040	*A. macrostachya*	natural	native	deciduous	tree
Senegal, Casamance	1 040	*Eucalyptus camaldulensis*	planted	exotic	evergreen	tree
Cameroon, north	1 080	*A. polyacantha*	planted	native	deciduous	tree
Cameroon, north	1 080	*Cassia siamea*	planted	exotic	evergreen	tree
Cameroon, north	1 080	*E. camaldulensis*	planted	exotic	evergreen	tree
Congo, Kouilou	1 250	Eucalyptus hybrid PF1	planted	exotic	evergreen	tree
Congo, Kouilou	1 250	Eucalyptus hybrid HS2	planted	exotic	evergreen	tree

Acacia macrostachya: respiration not measured.

NaOH which was determined with 0.1 N HCl. Air circulation was followed by the percolation of 60 mL water before the tube was closed again, in order to simulate leaching by rain and prevent dissolved compound accumulation. Dissolved carbon and dissolved phenolics were measured in the percolates. It was shown on some species that two or three replications gave close results (*figure 1*) the mean results of which were used, while most species were studied with one replication.

3. RESULTS

The significance probability of the results is given at the 5 % risk level. Chemical composition was highly variable between litters (*table II*) which showed a large range of quality.

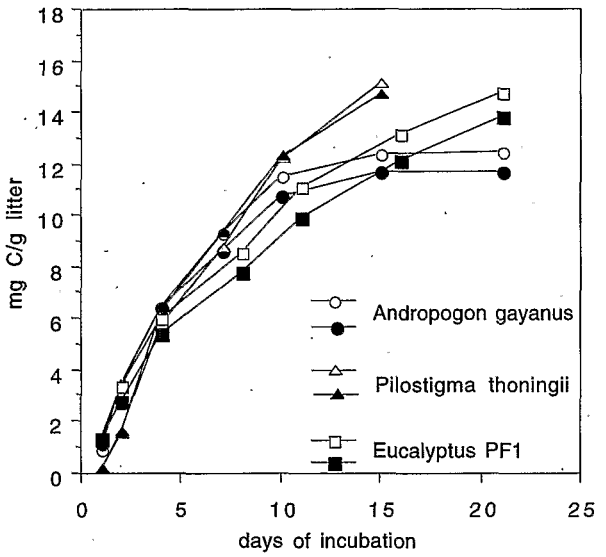

Figure 1. Examples of replications of CO_2 release measurement during 21-d incubations of leaf litters.

The total amounts of leached C recovered in percolations ranged from 10 to 55 % of the initial soluble C, and of leached phenolics from 3 to 30 % of the initial soluble phenolics (with an exception of 56 %), and were correlated with the initial contents. Most was leached during the three first days of incubation except for *Eucalyptus* where soluble compounds were recovered over a longer period.

The total release of CO_2 during 21 d ranged from 3.5 to 15 mg C per g of litter, i.e. approximately 0.7–3 % of litter C (*table III*). No significant relationship was found with any initial compound content.

Some of the cumulative curves of CO_2 release are given in *figure 2* and show various patterns according to species. They appeared to be composed of two approximately straight curves, one for the two first days and one from 7 to 21 d, with an intermediate curved part. The slope of the regression was calculated for 1–2-d and 7–21-d periods. The most obvious result was that the factors which control carbon mineralisation rate was not the same during the two stages. Correlation coefficients between chemical data and CO_2 curve slopes were calculated and the significant relationships are given at *table IV*. Relationships with phenolic compounds are shown in *figure 3*.

However, the various compound contents were correlated between them (*table V*). A step-by-step multiple regression showed that only insoluble phenolics was significantly related with the first stage rate, and only soluble C/soluble N ratio was significantly related with the second stage rate.

4. DISCUSSION

The amount of water used for each percolation accounts for a rainfall of 24 mm, i.e. 168 to 192 mm

Table II. Chemical characterisation of initial litters expressed as per amount of oven-dry matter and limb thickness.

	Sol. C (%)	Sol. C/sol. N	Total N (%)	ADF (%)	ADL (%)	Sol. phen. (%)	Insol. phen. (%)	Thickness 0.01 mm
Fallow grasses (Sine Saloum)	18	20	0.32	56	8	5	8	20.7
Fallow grasses (Casamance)	22	24	0.56	52	11	9	5	17.0
Andropogon gayanus	36	61	0.38	49	7	4	12	19.9
Guiera senegalensis	38	36	1.55	64	38	24	20	30.7
Combretum glutinosum	102	72	0.74	27	8	16	16	23.5
C. geitonophyllum	75	34	0.67	44	23	31	72	35.2
Terminalia macroptera	84	143	0.68	50	20	116	15	29.8
Pilostigma thoningii	67	122	0.81	55	29	29	110	49.6
Acacia holosericea	73	59	1.03	38	23	58	78	57.2
A. polyacantha	49	29	2.20	55	35	17	51	19.2
A. macrostachya	54	49	1.75	48	27	33	46	19.0
Cassia siamea	73	38	1.18	27	12	22	11	20.5
Eucalyptus camaldulensis S	115	90	0.67	27	12	86	14	nd
E. camaldulensis C	91	80	0.70	31	12	66	12	35.4
Eucalyptus PF1	108	155	0.65	35	22	123	50	35.0
Eucalyptus HS2	93	112	0.67	nd	25	116	44	30.0

sol. C, Soluble C; sol. N, soluble N; sol. phen., soluble phenolics; total phen., total phenolics; insol. phen., insoluble phenolics.
Eucalyptus camaldulensis: S = Senegal, C = Cameroon.
nd, Not measured.

Table III. C-CO_2 release data. C-CO_2/21 d: cumulated release mg C/g initial litter. C-CO_2 release rates: slopes of the graphs.

	C-CO_2/21 d	C-CO_2 release rate/1–2 d	C-CO_2 release rate/7–21 d
Fallow grasses (Sine Saloum)	12.8	3.64	0.160
Fallow grasses (Casamance)	13.1	2.76	0.372
Andropogon gayanus	11.6	2.37	0.224
Guiera senegalensis	13.8	3.01	0.297
Combretum glutinosum	13.8	4.67	0.490
C. geitonophyllum	16.3	1.10	0.428
Terminalia macroptera	20.0	4.60	0.968
Pilostigma thoningii	15.2	1.49	0.760
Acacia holosericea	9.8	0.19	0.385
A. polyacantha	16.9	3.65	0.450
Cassia siamea	15.3	3.98	0.300
Eucalyptus camaldulensis S	22.5	3.86	0.709
E. camaldulensis C	18.1	2.70	0.597
Eucalyptus PF1	14.0	2.04	0.821
Eucalyptus HS2	15.5	2.05	0.794

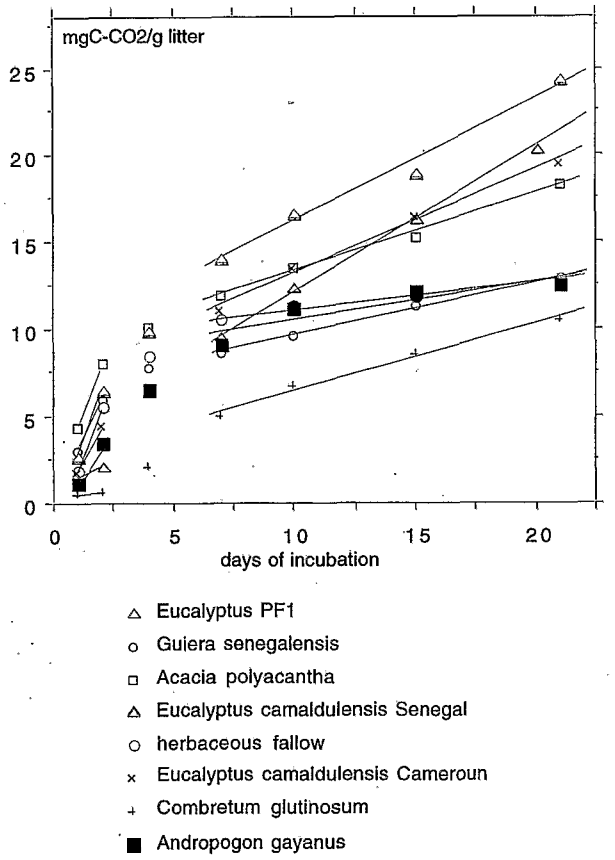

Figure 2. Carbon release as CO_2 during 21-d incubations of eight leaf litters from the fourteen studied.

during 21 d which is unlikely to occur usually in Sahelian and Sahelo-Soudanian regions, and it may be assumed that leaching of organic compounds in the field is lower. However, less than half of the organic soluble compounds are leached during the studied stage of decomposition and the remaining compounds may provide substrates for C mineralisation.

The shape of CO_2 release versus time curves is dependent of the experimental time step, as shown by hour-based measurements [14] or long time measurements [25, 17]. With the day-based measurements of the present study, the curves showed two stages. The first stage corresponds to the decomposition of the most easily degradable compounds, generally assumed to be sugars, starch and low molecular weight extractives [9]. Studying kinetic fractions, Marstorp [14] showed that the first one corresponded to glucose, fructose, sucrose, free amino acids and perhaps fructane, and was mineralised approximately during the first 24 h. Our results suggest that, when different species are considered, the CO_2 release rate during the early stage was not related to the amount of available soluble carbon. The main controlling factor was the inhibition by insoluble phenolics, which might be related to the antimicrobial effect of some polyphenols which provide resistance to bacteria and fungus [11], and leaf thickness. Negative correlation with leaf thickness might be related to its correlation with insoluble phenolics, and to the lower accessibility of leaf cells to microflora in thick leaves. Leaf thickness appears to be related to phenology, as shown by the significant difference in mean thickness (probability 0.009) between deciduous and evergreen species.

During the second stage, the CO_2 release rate decreased sharply and exhibited a close positive correlation with initial water soluble phenolics, or the remaining phenolics at the end of the experiment, which are mainly simple and low molecular weight phenolics. Although polyphenols have been shown to be very resistant to degradation [26], low molecular weight phenolics may be more easily degraded but little is known on phenolic compound degradation [10, 11]. However, at this stage, the most significant relationship occurred between respiration rate and soluble C/soluble N ratio, which may be assumed to be an indicator of the degradability of litter organic compounds.

Neither 'Van Soest' lignin nor total nitrogen effects were apparent during the incubation period. The influence of lignin on CO_2 release was shown with longer incubations by Robin [25] studying various organo-mineral products and by Vanlauwe et al. [27] with tropical tree species. Lignin is among the last compounds to be degraded, and although, it prevents cellulose accessibility to microorganisms, it might have little influence in the early stage. Nitrogen was shown to be correlated with total CO_2 release in long-term measurements [17] but Vanlauwe et al. [27, 28] did not find any relationship. In the present study, nitrogen was not the most limiting factor for microflora.

Studies on field decomposition and top soil organic matter are going on in order to check their correlation with laboratory incubation studies and will assess the

Table IV. Correlation coefficients, *r*, and error probability for the relationships between the significant initial chemical characteristics of litter and CO_2 release curve slopes.

	First and second days		7th to 21st days	
	r	Error probability	*r*	Error probability
Soluble C	0.031	ns	0.715	0.003
Remaining soluble C*	–0.308	ns	0.688	0.004
Soluble C/soluble N	0.078	ns	0.907	0.0001
Soluble phenolics	–0.108	ns	0.844	0.0001
Remaining soluble phenolics*	–0.133	ns	0.825	0.0002
Total phenolics	–0.495	0.06	0.809	0.0003
Insoluble phenolics	–0.738	0.0017	0.040	ns
Total phenolics + lignin/N	–0.544	0.04	0.416	ns
Lignin/N	–0.547	0.03	0.021	ns
Leaf thickness	–0.739	0.025	0.379	ns

ns, Not significant.
*, Calculated as initial minus leached.

Table V. Significant correlation coefficients between the initial compound contents of litters. *, Error probability < 5 %; **, error probability < 1 %; ***, error probability < 1 %.

	Leaf thickness	Sol. C	Sol. C/sol. N	Sol. phen.	Total phen.	Insol. phen.	Total N
Sol. C							
Sol. C/sol. N		0.769***					
Sol. phen.		0.724***	0.856***				
Total phen.	0.733**	0.638**	0.776***	0.824***			
Insol. phen.	0.853***				0.667**		
Total N							
ADL	0.570*				0.413*	0.595**	0.770***

sol. C, Soluble C; sol. N, soluble N; sol. phen., soluble phenolics; total phen., total phenolics; insol. phen., insoluble phenolics.

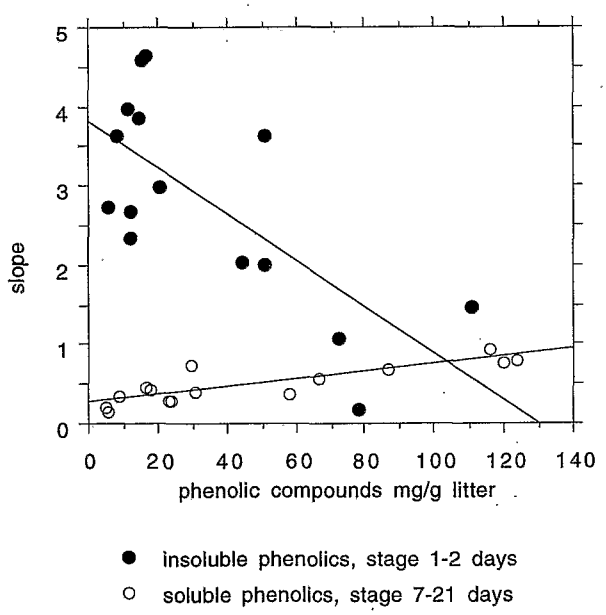

Figure 3. Respiration rate (slope of the CO_2 release curve) versus initial phenolic compound content in leaf litters for the two stages of litter respiration.

relationship between long lasting high respiration and lower organic matter input to the soil. Such an opposition was shown previously between *Eucalyptus camaldulensis* and *Acacia seyal* [3] by respiration measurement in old litter and organic matter content in top soil. Relationships between laboratory respiration and field decomposition is less likely to occur as field decomposition is measured through weight loss from litter bag, which is the sum of fragmentation and respiration.

Although species were chosen for their abundance in the studied sites independently from their chemical composition and although they covered a large range of litter quality, the choice may influence the results because the number of species is low. It would be interesting to obtain different polyphenol contents in a single species to study their influence on decomposition, as it was experimented for nitrogen by Marstop [15]. Variations in light and nutrient supply should be tried for this purpose as they are known to influence leaf polyphenol content [7, 16].

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