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Change in lignin content during litter decomposition in tropical forest soils (Congo): comparison of exotic plantations and native stands

Évolution de la teneur en lignine et décomposition de la litière dans les sols des forêts tropicales (Congo): comparaison de plantations exotiques et de peuplements naturels

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ABSTRACT

Fast-growing tree plantations are being extended in tropical countries resulting in new forest ecosystems, the functioning of which is yet not well known. In particular, few data are available concerning lignin decay rate. Lignin, nitrogen and tannin contents of fresh and decaying litter were measured in natural rain forest and in planted stands of *Eucalyptus* hybrids, *Acacia mangium* and *A. auriculiformis* in Congo, together with litter-fall and forest-floor accumulation. Lignin evolution in aging litter exhibited different patterns. Lignin was accumulated under Eucalyptus plantation, but disappeared under natural forest, and was intermediate under *Acacia* plantations. The relationships with decomposition rates and lignin degradation factors, such as white rot fungi and termites, are also discussed.

Keywords: *Rain forest,* Eucalyptus, Acacia, *Congo, Lignin, Litter, Decomposition*

RÉSUMÉ

Les plantations d'essences forestières à croissance rapide se développent dans les pays tropicaux, conduisant à de nouveaux écosystèmes forestiers dont le fonctionnement reste encore mal connu. En particulier, les données sur l'évolution de la lignine dans les litières sont très rares. Au Congo, les teneurs en lignine, azote et tannin de litières fraîche et en voie de décomposition ont été mesurées dans des forêts ombrophiles et dans des parcelles d'Eucalyptus hybrides, *Acacia mangium* et *A. auriculiformis,* et comparées aux chutes de litière. L'évolution de la lignine avec l'âge diffère selon le type de forêts. Elle s'accumule sous *Eucalyptus,* mais disparaît dans la forêt naturelle, les plantations d'*Acacia* représentant un cas intermédiaire. Les relations entre taux de décomposition des litières et facteurs de dégradation de la lignine sont également discutées.

Mots clés : Forêt ombrophile, *Eucalyptus, Acacia,* Congo, Lignine, Litière, Décomposition

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VERSION ABRÉGÉE

La lignine est un composé organique abondant dans les végétaux et les litières végétales, qui participe pour une part importante à la matière organique du sol, et que seul un nombre restreint d'organismes sont susceptibles de dégrader (Andreux et Munier-Lamy, 1994 ; Berthelin et al., 1994 ; Hammel 1997). Les mieux connus de ces organismes sont les pourritures blanches, mais les termites sont également capables de dégrader la lignine (Butler et Bucherfield, 1979). De plus, il a souvent été écrit que la lignine des litières en contrôle la décomposition, parce qu'elle fait obstacle à la dégradation de la cellulose (Sterjiades et Erikson, 1993). Toutefois, les relations entre vitesse de décomposition des litières et teneur en lignine ne sont pas toujours établies. Le but de cette note est de comparer le comportement de la lignine dans plusieurs écosystèmes forestiers tropicaux.

Les litières étudiées proviennent de la forêt ombrophile du Mayombe (Congo), et de plantations d'Eucalyptus hybrides et d'Acacias australiens faites sur le littoral, à une centaine de kilomètres de la forêt naturelle étudiée. Le climat de ces régions est subéquatorial, avec une pluviométrie moyenne annuelle de 1 250 à 1 500 mm, et les sols sont ferrallitiques fortement désaturés, sablo-argileux sous forêt et sableux sous plantations.

On a déterminé la teneur en lignine dans les fractions suivantes : la litière de feuilles fraîches récoltée dans des cadres (L1), la litière de feuilles anciennes peu fragmentées (L2) et la litière très fragmentée, qui est la plus ancienne (L3) – ces deux dernières fractions étant récoltées sur le sol. La détermination du coefficient de décomposition K = L1/(L2 + L3) permet d'estimer approximativement l'âge moyen des fractions par le rapport 1/K (tableau I).

Les litières fraîches ont des teneurs en lignine élevées (tableau II) par rapport aux résultats concernant principalement des litières tempérées (Meentemeyer, 1978). Toutefois, les litières d'Eucalyptus sont plus pauvres que les autres et selon Berendse (1994), cela pourrait être lié à une durée de vie courte des feuilles. On n'observe pas de relation entre la vitesse de décomposition et la teneur en lignine des litières fraîches. Cependant, une relation étroite entre la décomposition et le rapport lignine/N est mise en évidence si l'on exclut les litières d'Acacia, dont les teneurs élevées en azote résultent de la fixation symbiotique (figure 2).

L'évolution de la teneur en lignine avec l'âge des litières diffère selon les peuplements (figure 1). En forêt naturelle, la teneur reste constante entre L1 et L2. La disparition de la lignine, au même rythme que la perte de matière sèche, pourrait être due à la consommation par les termites, constatée lors d'expérimentations en sacs. Ensuite, la teneur en lignine diminue en L3, ce qui suggère l'intervention des pourritures blanches, dont la présence a été observée en forêt.

Dans les litières d'*Eucalyptus*, on observe une forte augmentation de la teneur en lignine entre L1 et L2, avec peu de changement entre L2 et L3, qui traduit une accumulation de la lignine au cours de la décomposition. Dans ces plantations d'*Eucalyptus*, la litière de feuilles n'est jamais consommée par les termites, et aucune pourriture blanche n'y a été observée au cours des travaux de terrain conduits pendant plusieurs années. L'absence des pourritures blanches pourrait être due à la forte teneur en tannins de ces litières (tableau III). Les tannins sont en effet connus pour leur effet inhibiteur sur ces champignons (Swift et al., 1979). Les plantations d'*Eucalyptus* semblent donc caractérisées par l'absence des principaux décomposeurs habituels de la lignine. Une dégradation ou consommation de ce composé n'interviendrait que dans la litière ancienne fortement fragmentée qui se décompose très lentement, par des agents qui ne sont pas connus. Les litières d'*Acacia* montrent également une accumulation de lignine dans la litière, suivie d'une dégradation plus rapide que sous Eucalyptus. Les termites ne consomment pas la litière de feuilles d'*Acacia*, et malgré un très faible taux de tannins, n'observe que peu de taches de pourriture blanche.

1. Introduction

Lignin is a major component of plant litter, and is among the most recalcitrant compounds, and consequently is of major importance in soil humus building (Andreux and Munier-Lamy, 1994; Berthelin et al., 1994, Hammel, 1997). This phenylpropanoid polymer has a highly complex and variable structure. Its chemical determination is consequently not easy and different methods may lead to different results (Mangenot and Toutain, 1980). Because it constitutes a barrier preventing decomposition of cellulose, lignin content of litter has been reported to control litter decomposition rate (Sterjiades and Erikson, 1993). Melillo et al. (1982) and Stump and Binkley (1993) referred to the lignin/N ratio as a factor that is more related to decomposition than lignin content, and other authors did not find any relationship between decomposition rate and lignin content (Gillon et al., 1994). Other factors were shown to influence the activity of decomposers, particularly polyphenols or tannins (Bignand and Schaefer, 1980; Palm and Sanchez, 1990).

Lignin is known to have low degradability compared to other leaf components and its byproducts are incorporated in the soil humic acids (Stott et al., 1983). Only a restricted range of organisms, mainly Basidiomycete white rot fungi, were shown to be able to metabolize the intact lignin molecule (Swift et al., 1979), whereas the effect of brown rot fungi on lignin is less obvious and poorly understood (Hammel, 1997). A few studies reported lignin degradation by bacteria, but in experimental conditions only (Sterjiades and Erikson, 1993). However, some authors pointed out the role of termites in lignin degradation (Butler and Bucherfield, 1979), and it was emphasized later by Garnier-Sillam (1987) and Braumann et al. (1987), that endosymbiotic bacteria were responsible for lignin degradation by some termite species.

The aim of this study is to compare data on lignin content change during litter decomposition in natural and planted forests, together with initial nitrogen and tannin content data from the same sites.

II. Sites and methods

The study was carried out in two semi-deciduous rain forest sites, including six plots, located at Dimonika (2 plots, i.e., 1A and 1B) and Les Saras (4 plots, i.e., 2A, 2B, 2C and 2D) in the Mayombe region (Schwartz, 1993), and in four plots in 7-year-old fast-growing tree plantations established in the coastal area savanna, 70–100 km apart. The tree plantations included two hybrids of Eucalyptus (PF1 and HS2), *Acacia mangium* and *A. auriculiformis,* described by Bernhard-Reversat (1993). The climate of the area was described by Clairac et al. (1989). The region is submitted to a 4 month dry season with temperatures lower than during the rainy season, and with cloudy weather and high atmospheric humidity. Amounts of rainfall during the rainy season range approximately between 1 200 mm in the Eucalyptus zone and at Les Saras, and 1 500 mm at Dimonika, at an altitude of 400 m. All sites were located on ferralitic soils although the clay content was higher in the Mayombe sites.

Previous studies dealt with the amount of litter-fall and some decomposition processes in native rain forest and in artificial forests of exotic species in Congo (Bernhard-Reversat, 1993; Schwartz, 1993). Litter-fall was measured weekly in ten traps in each plot over 1 or 2 years. Traps were 1 × 1 m in forest plots and 0.5 × 0.5 m in plantations. Litter accumulation on soil (forest floor) was measured over 1 year in ten 0.5 × 0.5 m quadrats in each plot, twice a year in native forest where litter-fall was seasonal, and each month in plantations where litter-fall distribution was more even over the year. The results showed that litter-fall ranged between 4 and 6 t/ha/year under Eucalyptus and Dimonika forest, and between 8 and 10 t/ha/year under *Acacia* and Les Saras forest. It was irregular over the year and lower in December and January in plantation plots, and it was higher from July to September in native forest.

The following fractions were determined: fresh leaf litter (litter-fall = L1), forest floor leaf fraction > 4 mm (litter on the ground = L2) and fragmented forest floor litter 0.5–4.0 mm (fragmented litter on the ground = L3); in addition, the woody fresh litter (W1) and the woody forest floor litter (W2) were added for lignin determination. The decomposition coefficient was estimated according to Olson (1963) as $K = L1/(L2 + L3)$. An approximation of the mean age of the various fractions (table I), was calculated as $a = 1/K$ with $K = L1/L2$ for the age of the L2 fraction and $K = L1/(L2 + L3)$ for the age of the F2 + F3 fraction.

Lignin content was determined for each compartment on composite samples from all sampling traps and from 1-month collections. The results showed a relatively low variability among several sampling dates.

Lignin was determined by the Van Soest (1963) acid detergent method and tannin with the Folin-Ciocalteu reagent (Marigo, 1973) at the CIRAD-EMVT laboratory (Maison-Alfort, France). Nitrogen was determined by the Kjeldahl method at the ORSTOM analytical laboratory (Pointe Noire, Congo).

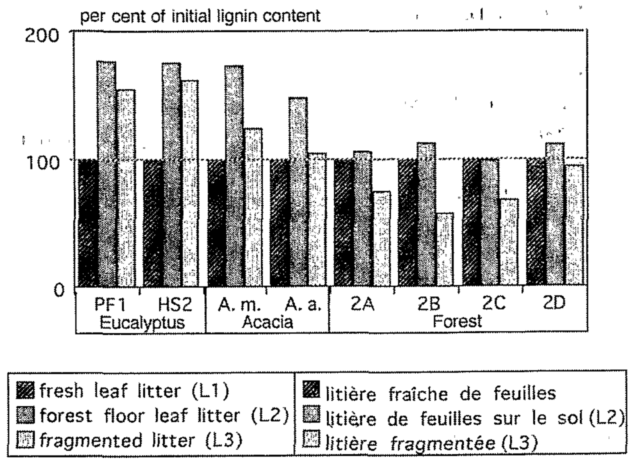

Figure 1. Lignin change with aging of leaf litter: lignin content of litter fractions, expressed as percentage of initial lignin content of freshly faller leaf litter.

Évolution des teneurs en lignine avec l'âge des litières, exprimées en pourcentage de la teneur initiale dans les litières fraîchement tombées.

III. Results

Analytical results are given in tables I–IV. In fresh leaf litter, lignin content was the highest in native forest and the lowest in *Eucalyptus,* while tannin content was considerably higher in *Eucalyptus* than in other litters (tables II and III).

Table I. Estimation of the mean age of litter fractions.

Estimation de l'âge moyen des litières.

Vegetation	*L1 (kg/ha/an)*	*L2 (kg/ha)*	*L2 + L3 (kg/ha)*	*Mean age L2 (year)*	*Mean age L2 + L3 (year)*
Eucalypt HS2	5.5	5.8	8.6	1.1	1.6
Acacia mangium	9.7	5.6	11.4	0.6	1.2
Acacia auriculiformis	10	5.3	10.4	0.5	1.0
Forest (mean)	6.1	4.3	—	0.7	—

Table II. Lignin content of litter, percentage of dry weight (and standard error).

Teneur en lignine de la litière, pourcentage de poids sec (erreur standard).

Fraction	*L1* *Fesh leaf litter*	*L2* *Floor leaf litter*	*L3* *Fragmented litter*	*W1* *Fresh wood litter*	*W2* *Floor wood litter*
Eucalypt PF1	**21.6 (1.2)**	**38.7 (0.7)**	**33.6**	—	**30.0**
Eucalypt HS2	**24.6**	**43.1 (3.2)**	**39.8 (2.5)**	**23.4**	**30.9**
A. mangium	**31.3**	**54.4**	**38.9**	**25.8**	**35.6**
A. auriculiformis	**34.2 (2.5)**	**50.8**	**36.1**	**34.8**	**37.3**
Forest 1 A	45.3	—	—		—
Forest 1 B	45.2		—	—	—
Mean forest 1	**45.2 (0.1)**	—	-	-	—
Forest 2 A	40.4	42.8	30.1	40.4	—
Forest 2 B	33.7	38.2	19.4	-	—
Forest 2 C	36.3	35.8	24.7	—	—
Forest 2 D	37.5	42.1	35.2	49.7	21.4
Mean forest 2	**37.0**	**39.7 (1.7)**	**27.4 (3.4)**	**45.0 (4.7)**	**21.4**

Table III. Tannin content of litter, percentage of dry weight.

Teneur en tannin de la litière, pourcentage du poids sec.

Fraction	*L1* *Fresh leaf litter*	*L2* *Forest floor leaves*	*L3* *Fragmented litter*
Eucalypt PF1	4.62	1.65	0.21
Eucalypt HS2	3.89	1.84	1.00
A. auriculiformis	0.75	—	
Forest 1 B	2.08	0.00	- -
Forest 2 A	1.20	0.48	0

Table II shows lignin content at various decomposition stages (fresh leaf litter, forest floor leaf litter, fragmented litter). The high lignin content of fresh leaf litter (L1) from native forest did not change between L1 and L2 and decreased sharply in L3. Unlike what was observed in natural forest, L2 and L3 litters from *Eucalyptus* stands had higher lignin content than L1, and in *Acacia,* only L2 had a higher lignin content than L1. The ratio of these values to the initial L1 value is given in figure 1 to make the comparison between stands easier. Lignin accumulates in *Eucalyptus* litter where it was not, or at least very slowly, metabolized. In *Acacia* stands, lignin accumulated in leaf litter and then disappeared faster than dry matter. In native forest lignin first disappears at the same rate as dry matter, and then faster than dry matter. If the age of litter fractions (estimated in table I) was to be considered, at the stage of decomposition, the difference in lignin evolution between *Eucalyptus* and forest should be increased.

The same trend was observed for the woody litter, the lignin content of which decreased from W1 to W2 during decay in natural forest, but it increased in *Eucalyptus* stands (table II).

It was obvious from table IV that the decomposition coefficient was not related to lignin content of fresh litter in the overall stands ($\rho = 0.312$), although in natural forest a higher lignin content was found with a lower K coefficient ($\rho = 0.797$, $p = 0.056$). Lignin content did not relate to stand production, expressed as annual litter-fall, when the overall stands were taken into account, but a significant inverse relationship between lignin content of L1 litter and total litter production was observed when *Eucalyptus* stands were excluded (figure 3). If the nitrogen-rich *Acacia* litters were excluded from the data given in table IV, a close relationship ($\rho = 0.938$, $p = 0.002$) was shown between lignin/N ratio of L1 and decomposition coefficient (figure 2).

Table IV. N percentage of dry weight and lignin/N ratio of the fresh leaf litter (L1), and decomposition coefficient of total litter in tree stands.

Pourcentage de poids sec N et rapport lignine/N de la litière fraiche (L1) et cœfficient de décomposition de la litière totale.

Plot	*N*	*Lignin*	*Lignin/N*	*Coef. K*
Eucalypt PF1	0.65	22	34	
Eucalypt HS2	0.67	25	37	0.24
A. mangium	1.62	31	19	0.76
A. auriculiformis	1.51	34	22	0.69
Forest 1 A	1.35	45	33	1.26
Forest 1 B	1.36	45	33	0.90
Forest 2 A	1.57	40	25	1.85
Forest 2 B	1.40	34	24	1.96
Forest 2 C	1.42	36	25	1.76
Forest 2 D	1.40	37	26	0.73

While sampling litter in the field, visual observations were made on white rot fungi. Spots of white rot fungi were not found under *Eucalyptus,* and they were scarce under *Acacia.* They were common in the Mayombe forest, although to a lesser extent than in some temperate forests (Toutain, pers. comm.).

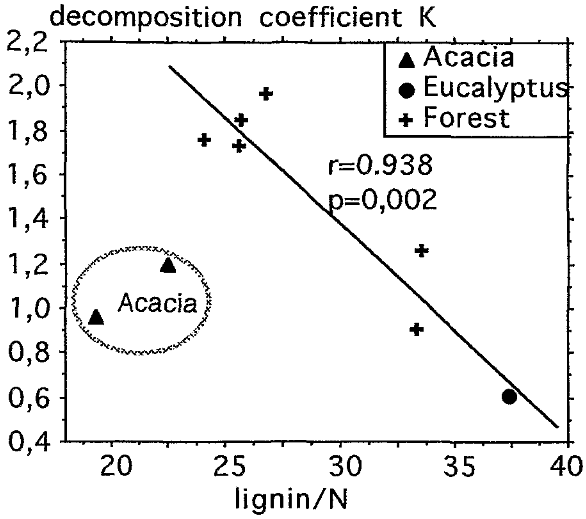

Figure 2. Relationship between the decomposition coefficient K and the lignin/N ratio of fresh litter (L1).

Relation entre le coefficient de décomposition K et le rapport C/N de la litière fraîche (L1).

the main factor contributing in the decrease in the turn-over rate in *Eucalyptus*. Palm and Sanchez (1990) suggest that tannins are the main factor controlling decomposition in senescent leaves of legume trees, because nitrogen content is high enough to result in a low lignin content, but this view does not fit with the *Acacia* studied here.

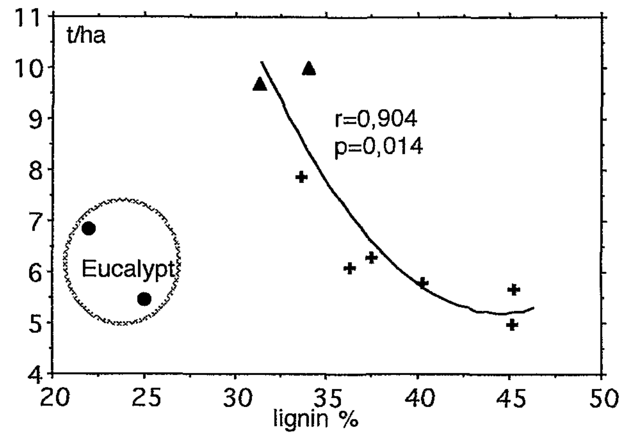

Figure 3. Significant binomial relationship between annual litter-fall and initial lignin content, excluding *Eucalyptus.*

Corrélation binomiale significative entre la chute annuelle de litière et la teneur initiale en lignine, excluant les Eucalyptus.

IV. Discussion

The overall values of lignin in litter were higher than most of those found in temperate litters (Meentemeyer, 1978) and in subtropical litter (Laishram and Yadava, 1988). As Ryan et al. (1989) found a good agreement between the Van Soest method and more complex methods in litter studies, this discrepancy was not attributed to the analytical method. Data from Anderson and Swift (1983) suggest that tropical forest litters had high lignin contents, close to those observed in the present *Acacia* and forest litters; however *Eucalyptus* exhibited a relatively low lignin content. According to these authors, and to Berendse (1994), high lignin content would be assigned to long-lived leaves, unlike deciduous ones. Comparison between litter-fall and tree leaf biomass in the studied *Eucalyptus* stands showed that, although *Eucalyptus* are evergreen trees, leaves lasted only 6 to 10 months (Bernhard-Reversat, unpublished data). In natural stands of *Eucalyptus diversicolor* from Mediterranean climate, lignin content ranges from 27 to 31% (O'Connell, 1988).

Lignin relationships with the decomposition rate were reported by other authors (Laishram and Yadava, 1988), while Melillo et al. (1982) and Parton et al. (1987) reported that lignin/N ratio controlled the amount of metabolic fraction in plant residues. Although this relationship was found by Taylor et al. (1989) to concern only lignin-poor litter, it also relates to the present lignin-rich litters, since they are nitrogen-poor. Our results (figures 2 and 3) suggest a very different behaviour of *Eucalyptus* and *Acacia* litter regarding lignin effect, and the major influence of the nitrogen and tannin content on lignin relationships. Although stand productivity might be related to a higher turn-over rate with lower lignin in litter, tannins might be

As was observed in litter-bag decomposition experiments (Schwartz, unpublished data), natural forest leaf litter was consumed by termites, which are the main decomposers in the Mayombe forest according to Garnier-Sillam (1987). Abe (1979) showed that some species of termites in tropical forest feed mainly on leaf litter. The first stage of decomposition of forest litter, where lignin is lost at the same rate as dry weight (figure 1), might tally with litter consumption by termites, while the second stage, when lignin is lost faster than organic matter, might involve the occurrrence of fungi. Limiting nitrogen conditions were shown to induce ligninolytic activity by white rot fungi (Sterjiades and Erikson, 1993) and could enhance lignin decomposition by fungi in F2 litter from natural forest.

Although numerous litter-bag decomposition experiments were carried out in the plantations, consumption of *Eucalyptus* and *Acacia* fresh leaf litter by termites was never observed. Termite frequency decreased in young *Eucalyptus* plantations, but termites were as frequent in older plantations as in natural savanna and forest (Bernhard-Reversat et al., 1996) and were observed in woody litter only. In Australian natural *Eucalyptus regnans* forest, Ashton (1975) did not quote termites among the soil fauna that disintegrated leaf litter, although termites were found at the site. Numerous observations of cultivated land generally have shown the occurrence of termite species from the nearby savanna, although with a decrease in biodiversity as compared with savanna, and many root feeding termites were found in other tree plantations (Rouland, pers. comm.). The reason for which termites do not consume plantation leaf litter is not known, and if tannin content may be put forward for *Eucalyptus* litter, *Acacia* litter exhibited a low tannin content.

According to Swift et al. (1979), white rot fungi are inhibited by polyphenols, as shown by several studies. The high tannin content of *Eucalyptus* litter as compared to forest litter (table III) could prevent the growth of white rot fungi. Without either termite consumption or white rot fungi activity, lignin is expected to accumulate.

V. Conclusion

Lignin changes in the litter of recently man-made forests were shown to be very different from that of native forest. In a previous study, Bernhard-Reversat (1993) suggested a poor adaptation of local soil biota to *Eucalyptus*. The long delay for lignin disappearance in *Eucalyptus* litter shown by the present data suggest that adapted lignin decayers could be among the lacking organisms, whereas lignin decayers should adapt to the exotic *Acacia* litter in the later stage of decomposition.

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