CHAPTER 2

THE LITTER SYSTEM IN AFRICAN FOREST-TREE PLANTATIONS

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ABSTRACT

Africa covers a wide range of climatic regions which give the opportunity to study a wide range of ecologically adapted tree species. Fast growing plantations are made with a reduced number of exotic species, whereas a greater variety of species are planted for timber, often chosen from local species. In the hierarchical model for the control of litter decomposition, climate is the higher factor in the hierarchy. In lowland plantations, temperature is not a limiting factor and the main climatic factor is rainfall, and litter quality will be the second factor in the hierarchy. The aim of the present study is to collect most of the available data on African plantations and to assess the main factors which influence litter dynamics, and the range of variability of the involved processes.

Tree species and rainfall are the main factors controlling litterfall, and litterfall in tree plantations is not basically different from litterfall in natural forests. Most exotic species have a low leaf litter nitrogen content and a high nitrogen use efficiency. Indigenous species have comparatively high nitrogen content. Lignin and phenolics vary with the tree taxa. Standing litter amount is related to climate and is low under dry climate due to low litter production, and in wet climate due to fast decomposition, whereas high amounts are found in medium climate with high production level and medium decomposition rate. Litter fauna generally changes with the establishment of plantations and is related to litter quality.

The decomposition rate is correlated with rainfall, and is not much different in exotic and indigenous plantations when annual rainfall is taken into account. Few data allow to exhibit relationships with litter quality.

Top soil organic matter which originates mainly from litter is highly related to climate and clay content. It appears to be related to the amount of standing litter which results from climate and litterfall. Standing litter could be a relevant measure to evaluate the functioning of the litter system.

Key Words: Africa, tree plantations, litter, soil organic matter.

The interest in studying litters in tropical forests is well established (Proctor, 1983, 1984, Vitousek, 1984) and litter dynamics in African tropical forests have been studied since many years ago (Bartholomew *et al.*, 1953, Nye, 1961, John, 1973, Madge, 1965, Proctor, 1984, Songwe *et al.*, 1988). Although special attention was paid at the beginning to nutrient cycling, the interest in carbon dynamics increased and is now important in litter studies (Schwartz, 1993). Studies on forests and tree plantation were undertaken together, however tree plantations received less attention. (Maheut and Dommergues, 1960). Concern for tropical forest protection and the increased need for land rehabilitation, wood production and pulp production, now emphasize the need for research on tree plantation ecology.

Africa, covering a wide range of climatic regions, from the dry Mediterranean and Sahelian to the wet equatorial, provides the opportunity of studying a wide range of ecologically adapted species. According to the aim of each plantation, those species are divided into fast-growing trees, which provide fuel wood, pulp wood, and are also used for land rehabilitation, and timber trees. Fast growing plantations are made with a reduced number of exotic genus, mainly eucalypts, pines and Australian acacias, which are selected for their growth rate, whereas a greater variety of species are planted for timber, often chosen among local species.

Lavelle *et al.*, (1993) proposed a hierarchical model for the factors controlling litter decomposition, where climate is the highest factor in the hierarchy. According to this model litter systems of highland plantations are highly variable, because temperature variations are dependent on altitude and control litter production and decomposition; consequently the amount of standing litter may show great variations in a reduced space (Morris, 1995, Dames *et al.*, 1998). In the present paper lowland plantations will be mainly considered. In lowland plantations, temperature is not a limiting factor and the main climatic factor is rainfall, and litter quality will be the second factor in the hierarchy (Lavelle *et al.*, 1993, Bernhard-Reversat *et al.*, 1998).

The aim of the present study is to collect most of the available data on African plantations and to assess the main factors which influence litter dynamics, and the range of variability of the involved processes.

Regarding numerous results, it was found relevant to sort the data into genus rather than into species. Eucalypt and pine plantations provide much more data than the other genuses, and their weight in the relationships described hereafter might result in distorted conclusions. However, in order to avoid this drawback an attempt has been made to check the relationships inside the genus.

THE LITTER SYSTEM IN TREE PLANTATIONS

FUNCTIONS OF LITTER

Litterfall serves three main functions in the ecosystem (Fig. 1): energy input for soil microflora and fauna, nutrient input for plant nutrition, and material input for soil organic matter building up. The first two functions are completed through decomposition and mineralization, and the third one through decomposition and humification. Those functions are related to the main soil processes, such as biological activity, nutrient cycling and soil structure.

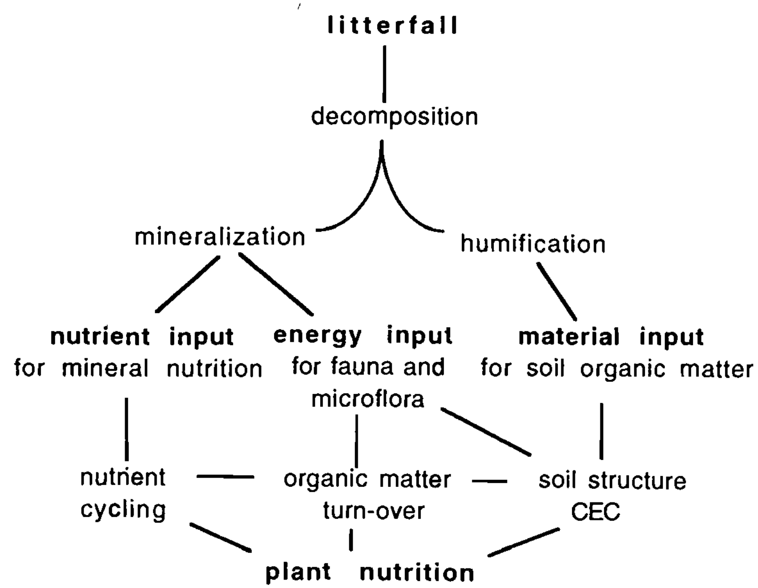

Fig. 1 Simple scheme of the main functions of tree litter.

PLANTATIONS COMPARED TO FORESTS

The characteristics of tree plantations may result in different litter forming processes as compared to natural forests. Tree plantations are generally monospecific and litterfall is dominated by one species, whereas tropical forests are very rich in plant species, at least in humid regions. Consequently the litter quality in tree plantations may lead to nutrient deficiency, extreme decomposition rates, or the accumulation of organic constituents resulting in toxicity for soil living organisms or to allellopathic problems (Chaturvedi and Jha, 1992, Lisanework and Michelsen, 1993, Bernhard-Reversat, 1999).

Sylvicultural practices modify the litter system. Plantations are generally exploited, resulting in nutrients losses by wood exportation and supplying a great amount of residues to the litter system, (Nwoboshi, 1980). Although fertilization is poorly used in African plantations it may bring nutrients. Those practices require nutrient cycling study in order to obtain a nutrient balance (Miller, 1984, Bouillet *et al.*, 1997a). Weeding is generally practised in young plantations and may change the litter system by burying the standing litter (Bouillet *et al.*, 1997b) or by spreading herbicides which may alter the microbial populations (Andariese and Vitousek, 1988).

LITTER INPUT TO THE SOIL (LITTERFALL)

QUANTITY OF LITTER

Data were collected from available publications on African tree plantations (Table 1). The amount of litterfall is different according to tree genera (Fig. 2), with the higher litter production for the nitrogen fixing Australian acacias, and the lowest production for conifers (pine

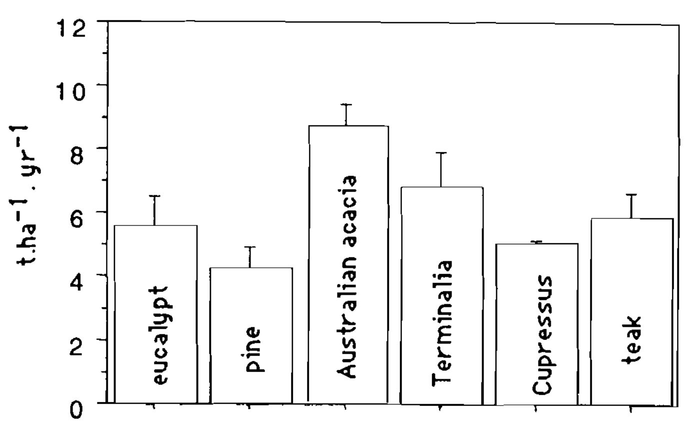

Fig. 2 Average annual litterfal in various genus of planted trees in Africa (data from Table 1).

and cypress) which are often planted in highlands. However a recent study in two plantations of *Pinus kesya* receiving high rainfall in Cameron showed higher litterfall (8.3 and 10.0 kg/ha/year) than the average given at the figure 2 (Njoukam *et al.* 1999). Neither the age of the planted plots nor the age of the trees are related to litter production when the whole data or one genus data are taken into account. However several studies showed that the litterfall of a given species in one site increases with age during and after the juvenile age (Kadeba 1998, Bernhard-Reversat *et al.*, 1999), but the age effect is hidden in the overall data, where variability is introduced by soil, climate and species.

Global relationship with the length of dry season was not observed, but the correlation with rainfall (Fig. 3) was significant (p=0.007). When pine or (eucalyptus) were considered alone, the relationships were still significant (p=0.04). The relationship of litterfall with rainfall was reported for tropical forest Jordan (1988) and according to Lonsdale (1988), precipitations give the best prediction model for leaf litterfall in tropical forests, whereas altitude give the best model for total litterfall, and when worldwide forests are considered latitude give the best model. Meentemeyer *et al.* (1982) find the better relationship with actual evapotranspiration (AET) but this parameter is rarely measured in studies on plantations.

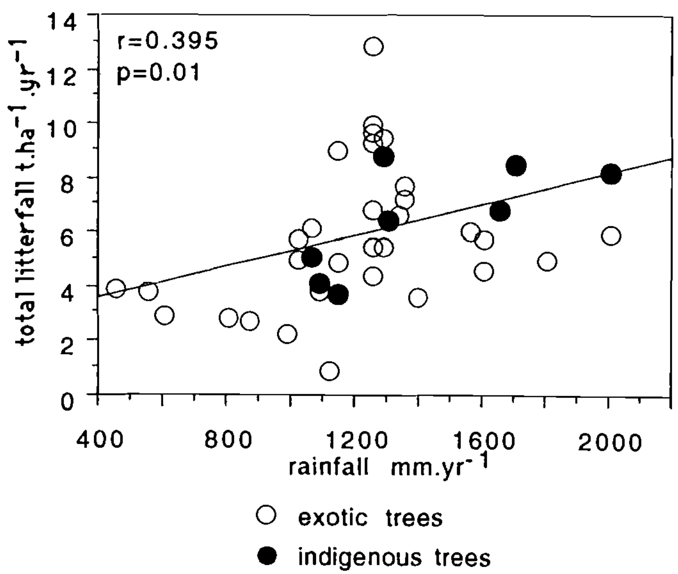

Fig. 3 Relationship between annual rainfall and annual litterfall in African tree plantations (data from Table 1).

Table 1 Data on African forest-tree plantations. K is the authors' value if available, if not K is the ratio litterfall/standing litter. Litter N content is given for leaf litterfall.

Authors	*Tree genus and species*	*Rain* mm/yr	*Plot age* yrs	*Litterfall /year* t/ha	*Litter N* %	*Standing litter* t/ha	*K*	*Top soil* C %
Bernhard-Reversat 1976	*Terminalia ivorensis*	2000	22	8.3	1.88	2.6	3.20	3.02
Bernhard-Reversat 1976	*Terminalia ivorensis*	1700	38	8.6	1.30	3.5	2.50	2.70
Bernhard-Reversat 1993	*Acacia mangium*	1250	7	9.7	1.66	12.0	0.69	0.92
Bernhard-Reversat 1993	*Acacia auriculiformis*	1250	8	10.0	1.65		0.69	0.92
Bernhard-Reversat 1993	*Eucalyptus HS2*	1250	7	5.5	0.65	10.3	0.35	0.71
Bernhard-Reversat 1993	*Eucalyptus PF1*	1250	10			15.5		
Bernhard-Reversat 1993	*Eucalyptus HS2*	1250	10			17.2		
Bernhard-Reversat 1993	*Eucalyptus PF1*	1250	7	6.9	0.66	14.0	0.49	0.71
Bernhard-Reversat *et al.*, 1999	*Eucalyptus PF1*	1250	19	9.4	0.75			0.73
Bernhard-Reversat *et al.*, 1999	*Eucalyptus PF1*	1250	19	12.9				0.78
Bernhard-Reversat unpublished	*Terminalia superba*	1300	32	6.5	1.30	4.6	1.40	1.26
Bernhard-Reversat unpublished	*Eucalyptus camaldulensis*	800	5	2.9	1.00	4.7	0.44	0.82
Bernhard-Reversat unpublished	*Pinus caribaea*	1250	10		0.25	15.9		0.59
Bernhard-Reversat unpublished	*Eucalyptus camaldulensis*	600	8	3.0	0.92	1.5	1.20	0.77
Egunjobi 1974	*Tectona grandis*	1140		9.0	0.89	4.5	2.02	
Egunjobi *et al.*, 1979 a,b	*Pinus caribaea*	1330	9	6.7		19.7	0.34	
Goubiere *et al.*, 1995	*Casuarina equisetifolia*	411	37			60.2		
Harmand 1997	*Acacia polyacantha*	1080	6	4.1	2.12	4.5	0.92	0.47
Harmand 1997	*Eucalyptus camaldulensis*	1080	6	3.9	0.71	12.6	0.39	0.35
Kadeba *et al.*, 1998	*Pinus caribaea*	1250	14	4.5	0.97	15.7	0.29	0.87
Kadeba *et al.*, 1998	*Pinus caribaea*	1800	14	5.0	0.88	17.2	0.29	1.67
Kadeba *et al.*, 1998	*Pinus caribaea*	1560	14	6.1	0.85	18.5	0.33	1.30
Kang *et al.*, 1994	*Treculia africana*	1280	10	8.8				0.96
Kang *et al.*, 1994	*Cordia alliodora*	1280	10	9.6				1.32
Kang *et al.*, 1994	*Gmelina arborea*	1280	10	5.5				1.20
King *et al.*, 1994	*Pinus patula*	885	40		0.83	25.7		0.91
King *et al.*, 1994	*Tectona grandis*	885	20		0.92	25.9		1.04
Knockaert 19 81	*Eucalyptus camaldulensis*	450	9	4.0		9.4	0.42	
Knockaert 1981	*Eucalyptus camaldulensis*	550	49	3.9		21.6	0.18	
Lisanework *et al.*, 1994	*Eucalyptus globulus*	1019	40	5.8	0.75		1.50	3.31
Lisanework *et al.*, 1994	*Cupressus lusitanica*	1019	28	5.0	0.60			3.56
Loumeto unbublished	*Okoumea klaineana*	1650	14	6.9	3.13	2.2	3.15	1.40
Lundgren in Vitousek 1984	*Cupressus*	1060	18	5.2				
Lundgren in Vitousek 1984	*Pinus*	1060	18	6.2				
Maheut *et al.*, 1960	*Tectona grandis*	1600	4	5.8	0.66			0.96
Maheut *et al.*, 1960	*Tectona grandis*	1600	8	4.7	0.94			1.10
Mailly *et al.*, 1992	*Casuarina equisetifolia*	525	34			120.3		0.23
Mailly *et al.*, 1992	*Casuarina equisetifolia*	525	6			23.1		0.08
Nwoboshi 1980	*Tectona grandis*		25	5.0		9.0	0.56	3.02
Ola-Adams *et al.*, 1992	*Tectona grandis*	1140*	18	5.0				
Ola-Adams *et al.*, 1992	*Terminalia*	1140*	13	3.8				
Oliver *et al.*, 1994 unpublished	*Acacia auriculiformis*	1350	5	7.3				1.99
Oliver *et al.*, 1994 unpublished	*Acacia mangium*	1350	5	7.8				1.99
Ronde 1993	*Pinus radiata*	620**	20			14.2		
Ronde 1993	*Pinus radiata*	620**	32			19.4		
Tie Bi and Omont, 1987	*Hevea brasilliensis*	2000	20	6.0		1.2	5.00	1.85
Versfeld and Donald, 1991	*Pinus radiata*	1390	50	3.7	0.64	6.6	0.55	
Wienand and Stock, 1995	*Pinus elliottii*	1113	28	1.0		1.0	1.00	
Wienand and Stock, 1995	*Pinus elliottii*	868	20	2.8		14.0	0.21	
Wienand and Stock, 1995	*Pinus elliottii*	980	25	2.3		7.0	0.35	

*data for Ibadan from Egunjobi 1979. ** data from the Weather Bureau of South Africa for Port Elizabeth.

Tree species and rainfall are the main factors controlling litterfall, and other factors related to sylvicultural practices seem to be less relevant; for instance, a study of the spacing effect in timber plantations in Nigeria did not show any significant difference (Ola-Adams and Egunjobi, 1992)

Litter Quality

Litter quality refers to mineral nutrients as well as to organic compounds and physical features, and is more often studied in leaf litter than in total litter. In plantations, leaves account for the most part of total litter, although bark and twigs may be important in some tree species. Nutrient content is often studied for mineral cycling assessments and organic compounds are being included into recent decomposition studies; physical characteristics are exceptionally taken into account.

Physical Characteristics

The easiest physical feature of litter to be measured is leaf thickness. Two examples of measurements made between the nervures with a thickness gauge by 0.01 mm, one with Australian acacias planted in Senegal, and the other with clones of two eucalypt hybrids planted in Congo, showed that leaf thickness was very significantly different between taxa, here species, hybrids or clones (Fig. 4); in eucalypt, leaf thickness was correlated with in vitro respiration and nitrogen content.

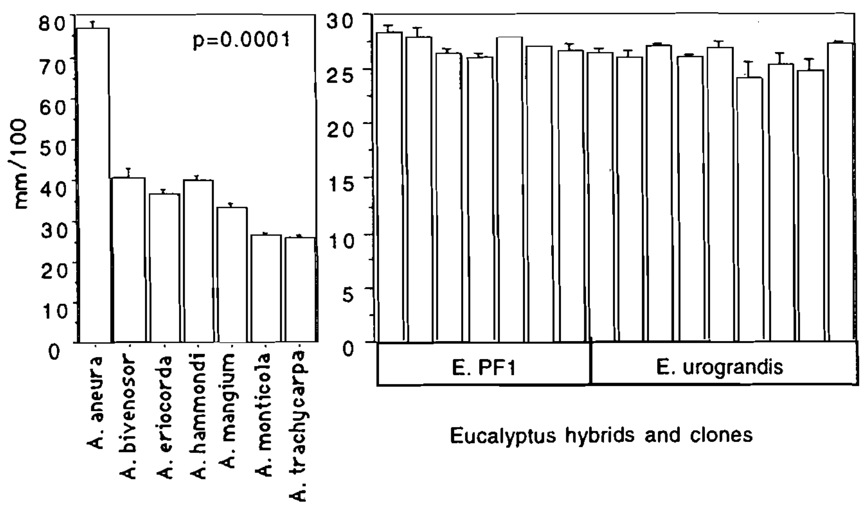

Fig. 4 Leaf blade thickness of litter in various Australian acacias planted in Senegal (left) and in various clones of Congolese eucalypt (right). Means of 10 leaves, measured on moisturized leaves.

Nitrogen Content

Nitrogen content of leaf litter, although expressed as mineral, is the expression of protein content, an important component for litter quality, and is discussed here. The main factor of leaf litter nitrogen variations is tree genus (Fig. 5A) and the ANOVA is highly significant ($p<0.0001$). Most exotic species are fast growing, and, except nitrogen fixing species, they have a low nitrogen content and a high nitrogen use efficiency (Chapin, 1980, 1983, Smith *et al.*, 1998). Indigenous species have comparatively high nitrogen content. Because of this great variability among genera, other controlling factors are not observed when the whole data are taken into account. However the nitrogen content of eucalypt leaf litter is highly correlated to rainfall: the highest the rainfall the lowest the nitrogen content. Faster tree growth and lower soil nitrogen content could explain this relationship, which is not observed in pine (Fig. 5B).

Organic Compounds

Litter organic compounds are considered to explain decomposition process in temperate as well as in tropical litter (Couteaux *et al.*, 1995, Spain and Le Feuvre, 1987, Cadish and Giller, 1997). Tree plantations received little attention with scarce data (Palm and Sanchez, 1991). The most common compounds which are considered are: soluble organic compounds susceptible to undergo leaching by rain, secondary metabolites including phenolic compounds and tannins, and the leaf fibers, cellulose and lignin. Some interest is sometimes given to terpenes which are assumed to act as allelopathic agents (Del Moral and Muller, 1969).

Data available on litter quality in African tree plantation is scarce. Organic compounds in litters of acacia and eucalypt were measured according to the methods described by Bernhard-Reversat (1999). It was observed that lignin content varied according to genera and was lowest in eucalypts (Fig. 6). Surprisingly, lignin content appears to be closely related to annual rainfall if nitrogen fixing trees are sorted out, and this relationship is still highly significant if eucalypts alone are considered (Fig. 7); this suggests that when water does not limit photosynthesis, an increased synthesis of secondary metabolites occurs (Matsuki, 1997), including those which are at the origin of lignin synthesis; this possible relationship would deserve more investigations, and could be supported by the positive relationship between water-soluble phenolics and rainfall in eucalypt leaf litter ($p=0.05$), and between methanol soluble phenolics (measured according to Anderson and Ingram, 1993) and rainfall in Australian acacia leaf litter ($p=0.003$).

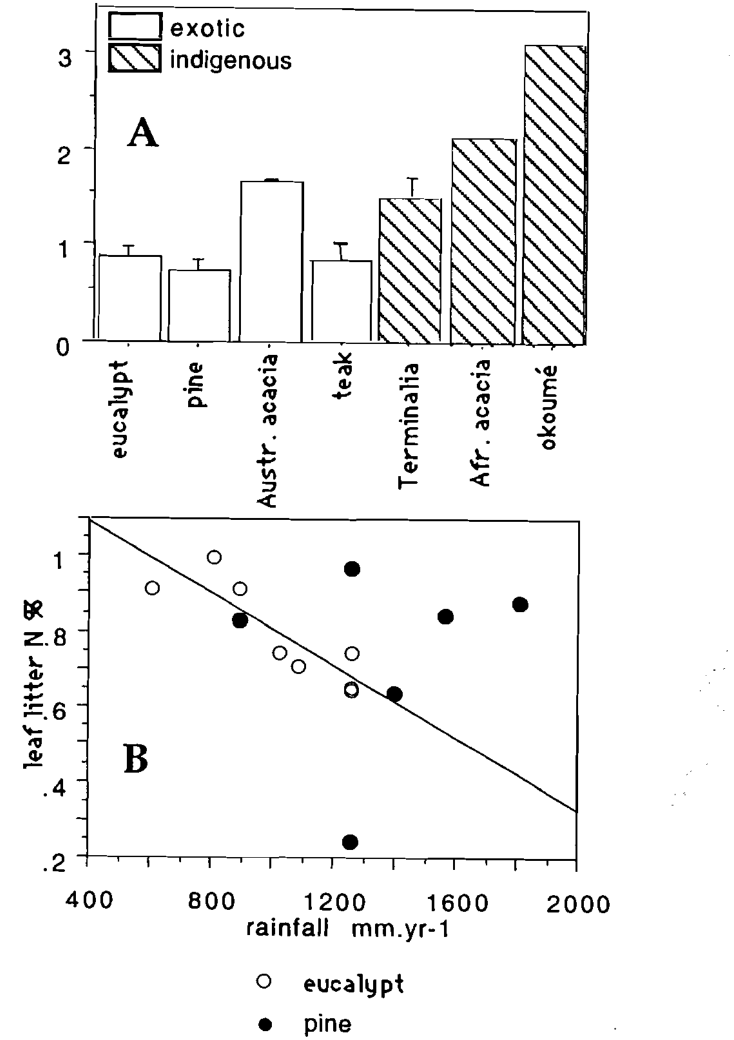

Fig. 5 Leaf litter nitrogen content. A: in various tree genus; B: relationships with annual rainfall in African eucalypt and pine plantations (data from Table 1).

NUTRIENT INPUTS THROUGH LITTERFALL

Nutrient cycling occurs mainly through litterfall and throughfall and except for potassium in wet forests, litterfall is the main pathway. Nutrient input to the soil by litter in African plantations received much attention (Maheut and Dommergues, 1960, Bernhard-Reversat, 1976,

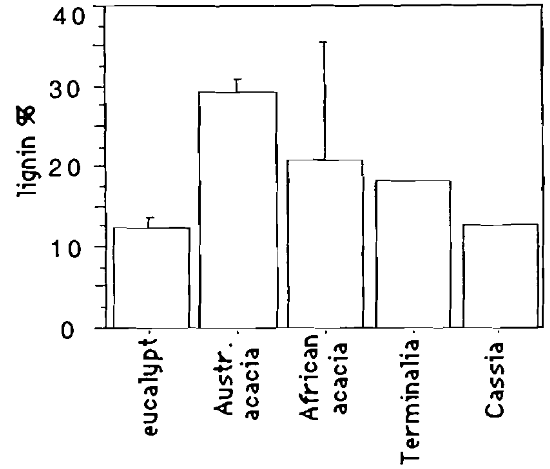

Fig. 6 Lignin content in the leaf litter of some tree genus in African plantations.

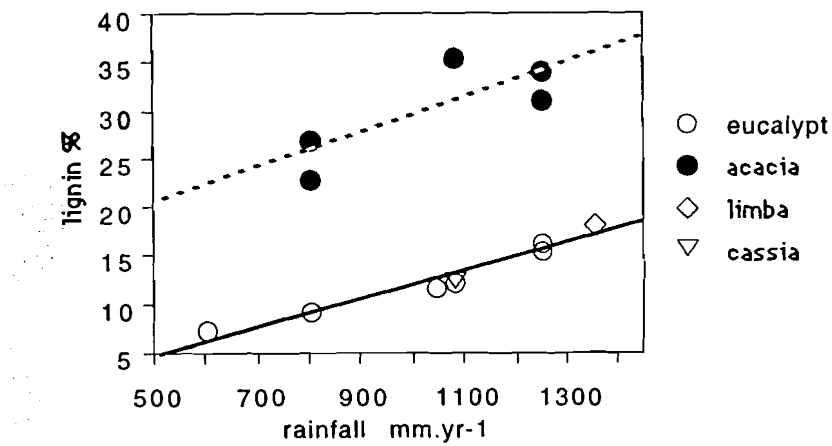

Fig. 7 Lignin content in leaf litter versus annual rainfall. Regression curves for acacias (broken line, not significant) and for other trees (solid line, $r=0.974$, $p<0.0001$) in African plantations (data from Bernhard-Reversat, 1997 and unpublished, Harmand, 1998).

1987, Nwoboshi, 1980, Kadeba and Aduayi, 1985, Loubelo, 1990, Kadeba, 1998, Laclau *et al.*, 1999; Njoukam *et al.* 1999); this interest is related to the occurrence of nutrient outputs by log exploitation. Nutrient input is more related to nutrient cycling than to the functioning of litter systems, and moreover a worldwide review was made by Vitousek (1984). According to this author litterfall is related to litter nutrient content for the residuals of climate regression, and plantations did not show different relationships from native forests.

STANDING LITTER ON THE SOIL

QUANTITY OF STANDING LITTER

The amount of litter on the ground in tree plantations is studied as an indicator of the litter system and the plantation functionning (Table 1). A particular case is that of the filao (*Casuarina equisetifolia*): this exotic tree is planted in dry littoral dune soils, which are free from organic matter and organisms, and litter accumulation is very high, up to 120 t/ha, because of the lack of decomposition (Mailly and Margolis, 1992, Gourbiere and Debouzie, 1995). Highland pine plantations in the Mediterranean mountain climate of South Africa also reach 100 t/ha (Morris, 1995). In tropical climate, excluding the results on filao, standing litter accumulation in plantations is significantly dependent on the length of the dry season (Fig. 8 A), with low accumulation under dry climate due to low litter production, low accumulation in wet climate due to fast decomposition, and high accumulation in medium climate with high production level and medium decomposition rate. Consequently

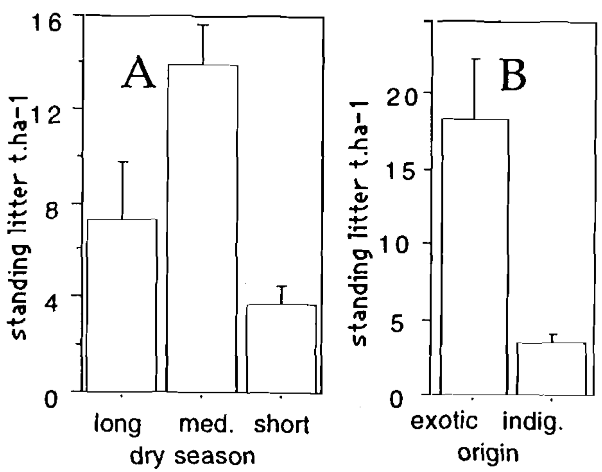

Fig. 8 Amount of standing litter on the ground according to the dry season (A), and to the origin of the species (B), in African plantation (data from Table 1).

no simple correlation can be observed between standing litter accumulation and rainfall. Where exotic species exhibit a wide range of standing litter amounts, the indigenous ones show low litter accumulation because their decomposing organisms are better adapted to the climate they live in, and the average accumulation is higher under exotic trees than under indigenous ones (Fig. 8 B).

QUALITY OF STANDING LITTER

Like for litterfall, data on the nutrient content of standing litter is given by authors studying biogeochemical cycling (Bernhard-Reversat, 1977, Nwoboshi, 1980, Loubelo, 1990, Harmand, 1997). Available data on organic quality is scarce although there is some natural tropical forests (McKey *et al.*, 1978). Nitrogen in particle size fractions of standing litter was shown to be related to initial litter content, and nitrogen content increases with decreasing particle size in nitrogen poor eucalypt and pine litters whereas it decreases in nitrogen rich acacia litters (Bernhard-Reversat, 1993).

Organic composition of standing litter is related to that of litterfall. However decomposition processes modify its composition, as shown by the comparison of lignin content in the standing litter of exotic plantations with that of natural forests in the Congo (Bernhard-Reversat and Schwartz, 1997); unlike in natural forests, lignin content increased in eucalypt standing litter compared to fresh litter, because of the lack of lignin-decomposing white rot fungi (Fig. 9).

LITTER ASSOCIATED FAUNA

Soil and litter fauna is the main factor of soil fertility (Lavelle *et al.*, 1993). Although both litter decomposition and litter incorporation to soil are dependent on meso and microfauna (Bocock, 1964; Reddy, 1995; Förster *et al.*, 1996, Pereira *et al.*, 1998), data available on African plantations is scant.

MESOFAUNA

Mesofauna is mainly made up of micro-arthropods. Tian *et al.* (1997) carried out decomposition studies in various vegetations at Ibadan, Nigeria, and assessed the microarthropod mediated decomposition to exhibit a higher rate in crop fields than in wooded stands because micro-arthropods mainly enhance microbial activity and are less important in stands which already have a high microbial activity. Bernhard-Reversat (1993) reported a highly significant increase in the number of micro-arthropods in plantations compared to the native

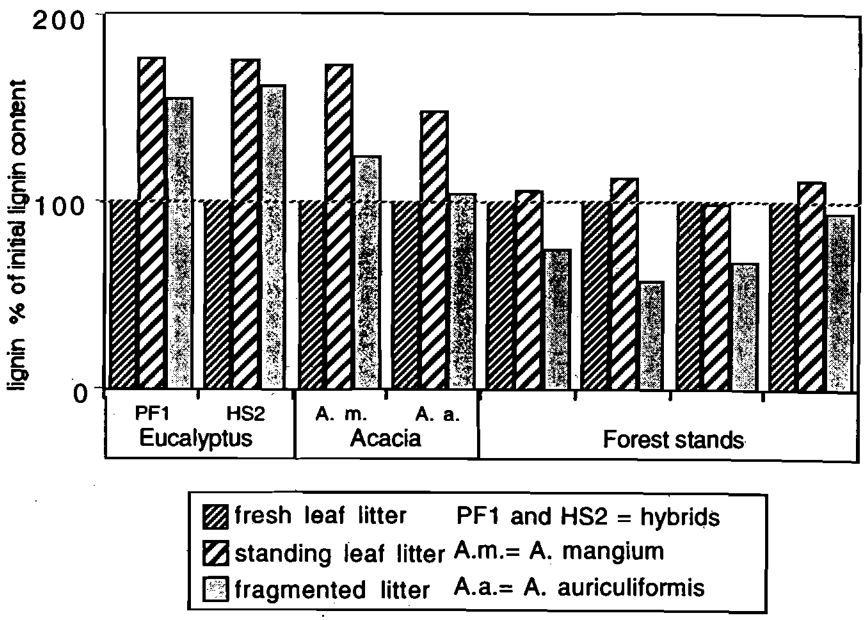

Fig. 9 Lignin content of litterfatl and standing litter fractions, expressed as per cent of the initial lignin content of freshly fallen leaf litter in Congolese plantations and forest stands. (after Bernhard-Reversat and Schwartz, 1997).

savanna in the Congo; no difference in micro-arthropod density occurred between eucalypt plantations and acacia plantations although the litter quality was better under acacia and seemed to increase the diversity of the morphotypes. Maldague (1961) showed that in Zaire the density of micro-arthropods was higher in artificial tree stands than in natural forests. Generally, forested environment appear to be more favourable to microfauna than open stands.

MACROFAUNA

A few studies were made on macrofauna and such data are available for plantations of rubber (Gillot *et al.*, 1995), eucalypt and pine (Dangerfield and Miller, 1996; Mboukou-Kimbatsa *et al.*, 1998), and Australian acacia (Mboukou-Kimbatsa *et al.*, 1998.)

Most results concern both litter and top soil, and show the change in macrofauna density in plantations compared to the native environment, either savanna or natural forest; those changes may concern total macrofauna or special groups as termites, earthworms or millipedes, which may be increased or decreased in density. In the Congo Mboukou-Kimbatsa *et al.* (1998) and Bernhard-Reversat *et al.* (1999) reported an increase in termite, earthworm, and litter group densities in eucalypt plantations of increasing age from 6 to 19 years whereas in the native savanna there were more termites than in plantations and no earthworms (Fig. 10). This increase in density with plantation age suggests an improved soil functioning with age. However in rubber (*Hevea brasiliensis*) plantations, Gillot *et al.* (1996) found that the litter group density increased from 5-year-old to 20-year-old stands, and decreased in a 30-year-old plantation together with decreasing tree productivity, whereas termites decreased since plantations were 10-years-old. The macrofauna population may find a favourable environment in plantation but the foregoing change in soil or litter quality may alter the environment conditions and the functioning of the system; macrofauna density could be a good indicator of the plantation's condition, although

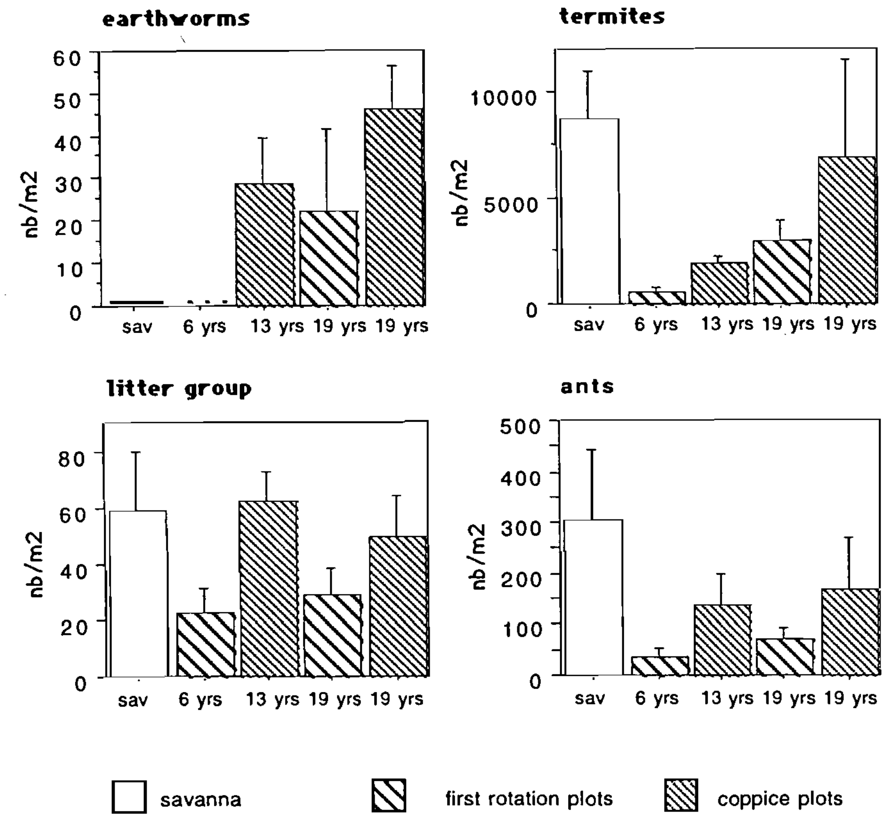

Fig. 10 Macrofauna densities in native savanna and in eucalypt plantations of various ages (Congo, data from Bernhard-Reversat *et al.* 1999).

more data is necessary. The influence of plant species on macrofauna was shown by Dangerfield *et al.* (1995) and Mboukou-Kimbatsa *et al.* (1998).

Relationships of Fauna with Litter Quality and Soil Quality

Litter quality is of critical importance in regulating soil and litter fauna and soil biological functions (Wardle and Lavelle, 1997, Tian *et al.*, 1997). Attempts to relate litter or soil macrofauna decomposing activity to litter quality in some African crops, mainly crop residues and agroforestry prunings, was made by Tian *et al.* (1993, 1995) who showed the important role of fauna in the decomposition of low quality litter. In the eucalypt plantations of the Congo, termites and ant densities were inversely related to the lignin content of the litter, and termite density was negatively correlated to the phenolic compound content (Bernhard-Reversat *et al.*, 1999). Nothing is known about plantations of indigenous trees. Although there is evidence that the monospecificity of the litter affects soil fauna in plantations, the detailed relationships and processes are unknown.

DECOMPOSITION

Litter decomposition received general attention in forest ecosystems including tropical ones (Anderson and Swift, 1983). Two field methods are mainly used, either comparison of litter input and litter standing crop, or weight loss measurements in litterbags.

Decomposition Coefficient

Since the theoretical basis of the calculation of the decomposition coefficient were assessed by Olson (1963) numerous authors used it in decomposition studies. The basic principle for mature tropical forests is to calculate the ratio "annual litter input/standing litter". Because of particular conditions some authors used other formulas (Bernhard-Reversat, 1982). In order to exploit the data of Table 1, we used the K value that was given by the author when available, or if not we used the previous ratio. The variability due to measurement or calculation methods does not prevent assessing some relationships.

The range of variations of K is very wide, from 0.2 in eucalypt plantations in Morocco, to 5 in a rubber plantation in Ivory Coast (Table 1). There is no relationship either with plot age nor with tree age. Genus, origin and climate control decomposition rate. Among the available results, pines and eucalypts have the lowest decomposition

rate, whereas the indigenous *Terminalia* showed a high decomposition rate (Fig. 11 A); however more data on planted indigenous species is necessary to check the difference between the low decomposition rate of exotic species and the high decomposition rate of indigenous species,

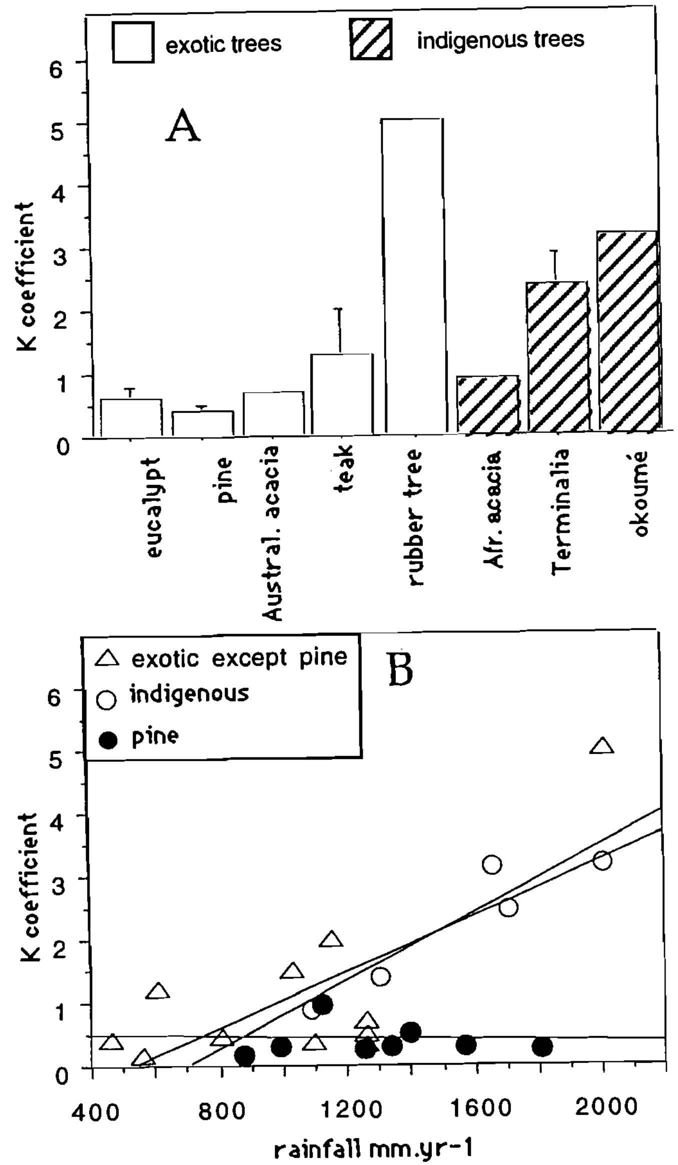

Fig. 11 Decomposition coefficient in African tree plantations: A, according to genus, B, related to rainfall (data from Table 1).

and the comparison is made difficult due to the scarcity of indigenous plantations in the dry regions where exotic species are most often planted.

Differences related to the length of dry season are highly significant (anova: $p<0.0001$) and are due to the high decomposition rate in short dry season stands. The averages for medium and long dry season are not different. The correlation with annual rainfall is significant ($p=0.02$) although pine litter decomposition seems not to be related to rainfall (Fig. 11 B), and the correlation is stronger ($p=0.0008$) when pine is not taken into account; macrofauna density is very low in pine litter and soil (Mboukou-Kimbatsa *et al.*, 1998) and the low decomposition rate of this litter could be due to either physical or chemical litter quality, although data available is little except evidence for low N content. In this case litter quality seems to prevail over climate, unlike in the hierarchical model (Lavelle *et al.*, 1993).

Litterbag Experiments

Litterbags are generally used to compare the decomposition rate of various tree species, to study the influence of macro and micro-fauna and to assess nutrient losses (Lisanework and Michelsen 1994; Loubelo 1990). However the ability of the litterbag technique to provide actual decomposition rate is questioned because weight losses are lower than calculated losses (Swift *et al.*, 1979, Bernhard-Reversat, 1982).

An attempt to put together the results of some litterbag experiments in African plantations is made (Table 2) using either the author's figures or data estimated from their weight loss curves, and percent weight loss at one, three and 12 months were compared. No correlation with the K coefficient occurs after one month decay, but it was observed after three and 12 months. However the litterbag experiments do not show any relationship with the studied factors suggesting that the resulting decomposition rates are highly dependent on sites, seasons and methodological protocols. Experiments conducted in eucalypt plantations in the Congo (Bernhard-Reversat *et al.*, 1999) reported a very significant effect of season; a significant increase of decomposition rate with plantation age was observed and could be related to the decreasing lignin content.

Decomposition and Litter Quality

The decomposition rate as measured by the K coefficient in Table 1 increases significantly with leaf litter nitrogen content ($r=0.623$, $p=0.006$) and a multiple regression shows that nitrogen content is more related to decomposition rate than to rainfall. Nitrogen content was shown to

Table 2 Weight loss per cent of initial weight in in litterbag decomposition compared to the decomposition coefficient K. Weight loss values are those givent by the authors when available, if not, they are estimated according to the authors' curves.

Authors	*Tree genus and species*	*rainfall* mm/ *year*	*weight loss % in 1 month*	*weight loss % in 3 months*	*weight loss% in 12 months*	*K (from table 1)*
Bernhard-Reversat 1987 and unpubl.	*Eucalyptus camaldulensis*	800	16	25	25	0.44
Bernhard-Reversat 1993	*Acacia mangium*	1250	21	37	60	0.69
Bernhard-Reversat 1993	*Eucalyptus PF1*	1250	18	25	44	0.49
Bernhard-Reversat 1993	*Eucalyptus HS2*	1250	11	15		0.35
Bernhard-Reversat *et al.*, 1999	*Eucalyptus PF1*	1250	26	32		
Bernhard-Reversat *et al.*, 1999	*Eucalyptus PF1*	1250	22	30		
Bernhard-Reversat unpublished	*Azadirachta indica*	600	29	44	44	
Bernhard-Reversat unpublished	*Eucalyptus camaldulensis*	600	18	36	36	1.20
Bernhard-Reversat unpublished	*Terminalia superba*	1300	13	60	100	1.40
Harmand 1997	*Eucalyptus camaldulensis*	1080			46	0.39
Lisanework *et al.*, 1994	*Eucalyptus globulus*	1019		30	82	1.50
Lisanework *et al.*, 1994	*Cupressus lusitanica*	1019		39	75	
Loumeto unpublished	*Okoumea klaineana*	1650				3.15
Versfeld and Donald, 1991	*Pinus radiata*	1390	8	14	29	0.55

be related to decomposition by several authors in temperate (Aber and Melillo, 1980) and in tropical environment (Laishram and Yadava, 1988), whereas climate is also reported as the main factor of decomposition (Meentemeyer, 1978, Aerts, 1997), and various factors are assumed to act at different decomposition stages (Couteaux *et al.*, 1995). The relationship of litter decomposition to litter organics, particularly lignin and phenolic compounds, were widely studied and some data is reported for other tropical vegetations (Constantinides and Fownes, 1994, Laishram and Yadava, 1988, Palm and Sanchez, 1991) but little is known on African tree plantations whereas data on agroforestry litters is available (Drechsel *et al.*, 1991, Vanlauwe *et al.*, 1996, 1997). In the Congolese eucalypt, Bernhard-Reversat *et al.* (1999) observed in a small number of plots that the decomposition rate was negatively correlated with lignin content during the dry season (p=0.03) suggesting that the lignin content of the litter could control faunal consumption when microbial activity is reduced by water limitation; results on other relationships with litter organic compounds were inconclusive because of the narrow range of variations inside eucalypts, and because decomposition rate increased with the age of plantations.

TOP SOIL ORGANIC MATTER

Through decomposition processes, the consequences of litter quality and quantity influence organic matter building up in the soil (Coleman *et al.*, 1989). According to Anderson and Flanagan (1989) the first hierarchical level of the processes is environmental control, followed by resource type and quality, then organisms, resulting in soil organic matter pool. These authors attribute different scales to this scheme and ecosystem, with total litter, controls total soil organic matter, whereas the composition of litter according to plant species controls patch variations in soil organic matter. We tried to check the influence of climate (rainfall), soil (clay content) and litter on soil organic matter content of some African tree plantations, from the data of Table 1.

The available data does not allow calculating anova for both texture and dry season length. Anova were made separately and are both highly significant (Fig. 12). Increasing annual rainfall increases C content in sandy soils (r=0.738, p=0.0009) but not in clayey soil; more data would be necessary to check these relationships.

The influence of climatic and soil conditions on soil organic matter makes the assessment of control processes by litter difficult; the relationships between soil organic matter and litter amounts are also influenced by litter quality. Neither the genus nor the origin of the trees

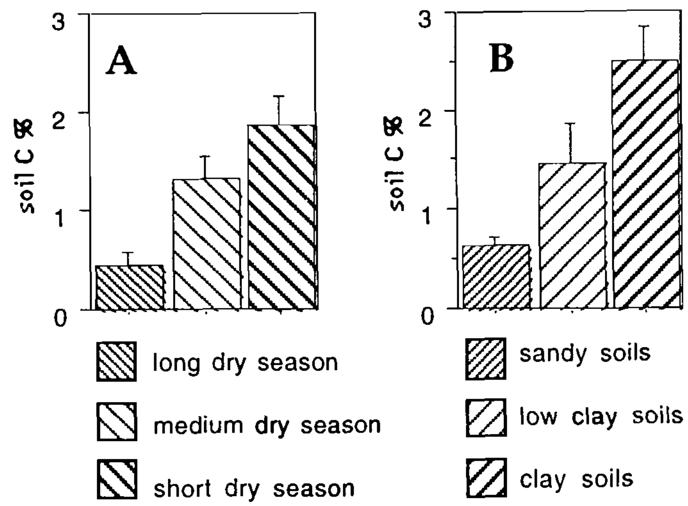

Fig. 12 Soil organic matter content according to the dry season length (A), and clay (B). Sandy soils: clay content < 10%, clay soils: clay content > 20%. Long dry season > 7 months, short dry season < 4 months. (data from Table 1).

is related to soil C with the above data. The age of the plantation (age since the plot was first planted) is well correlated to soil C (p=0.002) which accumulates throughout the years. When plantation age is taken into account in a multiple regression, the amount of standing litter, which result from litterfall and decomposition, is strongly negatively correlated to soil C (p=0.004) showing that low litter decomposition prevents the building up of soil organic matter. However relationships with accumulation can be more strong than relationships with decomposition in young stands under the same climate, and Kotto-Same *et al.* (1997) reported a positive correlation between standing litter stock and total soil C in a succession of fallows after cropping where soil C was mainly related to fallow age.

The light organic particle size fractions were related to the amount of standing litter in Congolese eucalypt plantation. Bernhard-Reversat (1993) showed considerable differences between particle size distribution of top layer soil organic matter under Australian acacia and eucalypt plantations in Congo, with a low level of the medium sized light fraction under eucalypt. The same difference was observed in Senegalese eucalypt plantations compared to neem *(Azadirachta indica)* and *Prosopis* plantations (Bernhard-Reversat, 1987) and refers to different origin and quality of the fractions (Boone, 1994, Gregorich *et al.*, 1996). This suggests that the humification processes are different according to litter quality, which controls the ratio comminution to mineralization.

CONCLUSION: TREE PLANTATIONS AND NATURAL FORESTS

Data on litterfall allows comparison between natural forests and plantations (Vitousek, 1984). Basically no differences appear between natural forest and plantations litterfall in Africa when annual rainfall is taken into account (Fig. 14) although local differences may be observed when the comparison is made on the same site (Table 3). In humid regions, litterfall of nitrogen-fixing fast-growing species and litterfall of timber plantations reach the same amounts than those of natural rain forests (Bernhard-Reversat, 1976, 1993). In dry regions litterfall of fast-growing species is greater than that of natural forest which are adapted to hard environment (Bernhard-Reversat, 1987).

Fast decomposition of organic matter and nutrient poor clays are common in tropical regions and soil organic matter is a very important factor of fertility. The litter system is the main pathway for organic matter from production by vegetation to soil humus. So the setting up of an indicator of the functioning of this pathway would allow

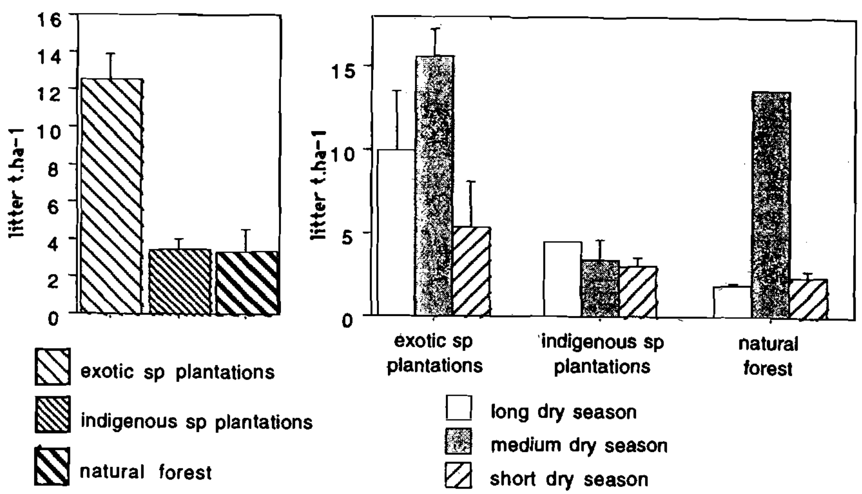

Fig. 13 Comparison of the amounts of standing litter on the ground in some plantations and natural forests (excluding *Casuarina*); A: all sites, B: according to the dry season length (excluding the South African mediterranean climate). (plantation data from Table 1, forest data from Greenland *et al.*, 1960, John 1973, Nye 1961, Madge 1965, Bernhard-Reversat, 1976 and unpublished, King *et al.*, 1994).

Table 3 Comparison of litterfall in tree plantations with litterfall in natural forest on the same or nearby sites

Authors	*dd*	*Rainfall* mm/yr	*Natural forest*	*Tree plantation*
Bernhard-Reversat 1987	Senegal	800	1.9	2.9
King *et al.*, 1994 (leaf litter)	Zimbabwe	885	2.72	3.27–5.08
Bernhard-Reversat 1976	Ivory Coast	2000	9.1	8.2
Bernhard-Reversat 1976	Ivory Coast	1700	8.6	9.6
Schwartz 1993, FBR unpubl	Congo	1300	5.0–5.7	6.4
Lisanework *et al.*, 1994	Ethiopia	1020	10.9	5.0–6.5

evaluations and comparisons of forested ecosystems. The most relevant parameter for soil organic matter building up could be the amount of standing litter on the soil, which integrates litterfall and decomposition, and consequently the climate data, although the relationships are complex. The amount of standing litter is significantly higher in forest plantations than in natural forests. If the origin of the planted species is taken into account, the significance is higher (anova: $p=0.001$) and it is obvious that only plantations of exotic species are different from natural forest (Fig. 13 A); this is noticeable also when the length of dry season is taken into account although the little data does not permit

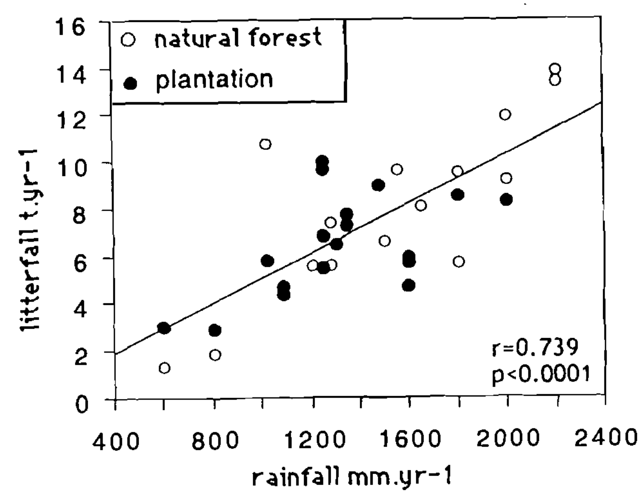

Fig. 14 Litterfall in some African forests and plantations versus mean annual rainfall (data from Table 1 and from Greenland *et al.*, 1960, Madge 1965, John 1973, Devineau 1976, Bernhard-Reversat 1977, 1987 and unpublished, Songwe *et al.*, 1988, Schwartz 1993 and personal comm.).

statistical comparison for each case (Fig. 13 B). This suggests that the adapted decomposers, microflora, mesofauna and macrofauna, are present in indigenous species stands, either planted or in natural stands, whereas some are lacking in exotic species stands. This is also suggested when African eucalypt plantations are compared to Australian natural eucalypt forests (Bernhard Reversat and Schwartz, 1997). The extreme is found in filao (*Casuarina*) plantations on sand dunes in Senegal, where in the absence of an organic soil few organisms decompose the litter, and decomposition was very low resulting in litter accumulation comparable to that of boreal forests (Gourbiere and Debouzie, 1995).

Although many studies have been conducted in tropical Asia and America, few have been reported on the litter system in African forests and plantations. Special attention must be paid to the chemical quality of the litter which plays a key role in the functioning of the litter system. Data collection on the quality of tropical organic resource is on with the aim of improving management of these resources (Gachengo *et al.*, 1998) and it may be assumed that more data on litter quality would contribute to more evidence of the dynamics of organic matter in African plantations and forests, and enhance our understanding of the processes controlling sustainability of tree plantations.

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