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Leaf decomposition in two semi-evergreen tropical forests: influence of litter quality

Gladys Loranger, Jean-François Ponge, Daniel Imbert, Patrick Lavelle

Institutions: University of Paris, University of the French West Indies and Guiana

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G. Loranger (corresponding author) · P. Lavelle

Université Paris 6 / IRD UMR BIOSOL, 32 Avenue Henri Varagnat, 93143 Bondy Cedex, France

E-mail: Gladys.Loranger@bondy.ird.fr

Fax: + 33.1.48.02.59.70

J-F. Ponge

Muséum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, 4 Avenue du Petit Château, 91800 Brunoy, France

D. Imbert

Université des Antilles et de la Guyane, Laboratoire de Biologie et de Physiologie végétales, BP 592, 97159 Pointe à Pitre Cedex, Guadeloupe, France

Abstract Decomposition processes are still poorly understood in tropical semi-evergreen forests. The influence of soil properties and litter quality on decomposition rate was studied in two semi-evergreen forests of Guadeloupe, a forest plantation and a secondary forest, located on different soils. Leaf litter of four tree species was enclosed in litterbags for a 14-month period. Non-linear correlations were calculated between mass loss and the concentration of major leaf components (soluble carbon, nitrogen, lignin, cellulose, tannins, total soluble phenols) in order to determine the best predictor of leaf litter decomposition. Soil physico-chemical properties and ratios between some of the above mentioned litter quality parameters were also examined as mass loss predictors. In addition, non-linear correlations were calculated between mass loss and litter quality parameters, at successive periods.

Litter quality was the main determinant of litter decomposition in the studied forests. Several litter quality parameters were correlated with leaf disappearance, varying according to stages of decomposition. Between 1 and 2.5 months, the mass loss was correlated negatively with the initial phenol content and with initial lignin : N and (lignin + phenol) : N ratios. From 2.5 to 5.5 months, the mass loss was correlated negatively with the initial phenol content and positively with the initial cellulose content. At later stages of decomposition (from 9 to 14 months), the mass loss was correlated negatively with the initial tannin content. Soil characteristics and faunal differences did not seem to be enough to affect decomposition.

Keywords Litter decomposition · Litter quality · Litterbags · Semi-evergreen tropical forests

Introduction

In terrestrial ecosystems, more than 90% of net above ground primary production returns to the floor as litter and constitutes the major resource for soil decomposers (Swift et al., 1979). Decomposition of plant litter includes leaching, break up by soil fauna, transformation of organic matter by micro-organisms and transfer of organic and mineral compounds to the soil. This process is mostly a biological but it is influenced by abiotic factors through their effects on soil fauna. Climate, soil characteristics, quality of decomposing organic matter and soil organisms are the most important factors regulating litter decomposition (Swift et al., 1979; Lavelle et al., 1993). However, in some climatic regions, and in the tropics in particular, litter quality parameters seems to be the best predictors of decomposition rates, whereas environmental conditions such as soil characteristics and microclimate tend to be less important (Meentemeyer, 1978 and 1984; Lavelle et al., 1993; Aerts, 1997).

The aim of numerous studies on litter decomposition has been to determine which characteristics of litter quality are the best predictors of decomposition rates. Initial N content and C:N ratio were the first litter chemistry parameters used to predict the rate of decomposition (e.g., Swift et al., 1979; Tian et al., 1992; Tripathi & Singh, 1992). Other studies have demonstrated that a strong negative linear relationship existed between short- and long-term decay rates and the lignin content, the ratio lignin : N, the phenol content or the ratio (lignin + phenols) : N (e.g., Meentemeyer, 1978; Palm, 1995; Aerts, 1997; Mesquita et al., 1998). Other studies showed that the long-term decomposition rate was increased by a high cellulose content (e.g., McClaugherty & Berg, 1987; Melillo et al., 1989). Other litter parameters have been shown to influence decomposition rates, such as toughness and cutin content (Gallardo & Merino, 1993).

For a better understanding of decomposition processes, models showing the influence of

substrate quality at different stages of litter decomposition have been developed. Two phases of the decomposition process have been determined, a leaching phase and a post-leaching phase, which are regulated by different litter quality parameters. McClaugherty & Berg (1987) suggested that in temperate forests, the first phase of the decomposition process (< 30% of initial mass loss) was regulated by the nutrient content, while the second phase was regulated by the lignin content and the holocellulose : lignin ratio. Gallardo & Merino (1993) found that in Mediterranean ecosystems leaf toughness and the ratio toughness : P were the best predictors during the leaching phase and cutin : N or cutin : P ratios were the best predictors of mass loss during the post-leaching phase. Such a work has never been carried out in tropical semi-evergreen forests, which are specific environments with a relatively long dry season and warm temperature.

In this study, we investigated the decomposition process of four types of leaf litter with contrasting chemical qualities, in two semi-evergreen forests of Grande-Terre (Guadeloupe) located on different soils. Our objectives were (1) to evaluate the relative importance of litter quality and soil characteristics for litter decomposition in tropical semi-evergreen forests and (2) to estimate the influence of different parameters of litter quality on decay rates, at different stages of the decomposition process, in these forests.

Materials and methods

Study site

The experiment was conducted in two semi-evergreen tropical forests, located in North Grande-Terre (Guadeloupe, French West Indies). The average annual rainfall is 1250 mm, 70% annual precipitation being concentrated in the humid season (June to November). Several species shed their foliage during the dry season, from December to May. Monthly rainfall is lower than 60 mm during February and March, the driest months. The mean

annual temperature is 26°C.

The first site is a secondary forest located on a shallow leptosol (FAO-UNESCO classification) on a steep slope with limestone bedrock. Main species of the canopy are Pisonia subcordata L. (Mapou gris) and Bursera simaruba (L.) Sarg. (Gommier rouge), which comprise 32% and 24% of the total basal area, respectively (Loranger, 1999). The second site is a 50-year-old forest plantation located on a calcareous vertisol on a plateau. Swietenia macrophylla King (Mahogany grandes feuilles) and Tabebuia heterophylla DC. Britton (Poirier pays) were planted for timber production. Both are used in cabinet making. At the present time, dominant canopy species are S. macrophylla, T. heterophylla and B. simaruba, which comprise 32%, 30% and 7% of the total basal area, respectively (Loranger, 1999).

Soil physico-chemical characteristics

Soil was sampled to a depth of 10 cm and placed in plastic bags. Percent moisture was calculated as [(fresh weight - dry weight) / dry weight] × 100 on 3 random soil samples in each forest, bi-monthly from February 1998 to December 1998 by considering weight before and after 72 h at 105°C.

In each forest, 10 soil cores of 40 cm depth were taken randomly. These cores were separated in several layers, 0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm depth. Samples were sieved to 2 mm, homogenised and chemically analysed. The pH_{H2O} was measured on a 10 g sub-sample diluted with 20 g deionised water, whereas the pH_{KCl} was measured on a 10 g sub-sample diluted with 20 g 1M KCl solution. The other analyses were performed on sub-samples sieved at 200 µm. Total C and N were determined with a CHN Carbo Erba® auto-analyser. Cation exchange capacity (CEC), exchangeable cations (Mg, K, Na) and primary nutrients (SiO_2, Al_2O_3, TiO_2, Fe_2O_3, K_2O, Na_2O, MgO, CaO, MnO, P_2O_5) were

also determined in both soils.

Soil texture was determined in each forest, in surface (0-10 cm in the secondary forest, 0-20 cm in the plantation) and deep layers (10-40 cm in the secondary forest, 20-50 cm in the plantation).

Mass loss determination

Decomposition of leaf litter of the main tree species of the canopy was studied using the litterbag technique (Bocock & Gilbert, 1957). Bags (20×20 cm stainless steel of 5×5 mm mesh) were filled with 10 g of dried recently fallen leaves. This large mesh size allowed most soil invertebrates to have free access to the content of the litterbags. One hundred and forty bags were placed under the corresponding tree species in both forests, at the soil surface. In the secondary forest, 28 bags were filled with P. subcordata leaves and 28 bags were filled with B. simaruba leaves. In the forest plantation, 28 bags were filled with S. macrophylla leaves, 28 bags were filled with T. heterophylla leaves and 28 bags were filled with B. simaruba leaves.

Four bags were randomly removed for each tree species at 14 days, 1 month, 2.5 months, 5.5 months, 9 months, 12 months and 14 months after the beginning of the litterbag experiment. After retrieval, each bag was placed in a separate plastic bag and transported to the laboratory. Litter samples were oven-dried at 65°C and weighted, then mass loss was calculated.

Chemical analysis of leaves

Freshly fallen leaves of the main canopy species, P. subcordata, S. macrophylla, T. heterophylla and B. simaruba, were collected from the forest floor. The leaves were air-dried and milled and the initial chemical composition was determined.

The total N content was measured with the Kjeldahl method. Soluble C compounds were extracted by mixing 2 g leaves with 60 mL cold water for 2 hours. Soluble C content in water extracts was then determined by the chemical oxygen demand (COD) using the HACH method (Jirka & Carter, 1975). Lignin and cellulose were analysed by sequential digestion of fibres (Van Soest, 1963). Samples were first extracted with neutral detergent. Lignocellulose ("acid detergent fibre" or ADF) was obtained after extraction with acid detergent. Lignin ("acid detergent lignin" or ADL) was obtained after hydrolysis with 72% H_2SO_4. Cellulose corresponded to the difference ADF-ADL. Total soluble phenols were extracted with 70% methanol then measured colorimetrically using the Folin-Ciocalteu method (Marigo, 1973). Tannins were measured with a colorimeter after precipitation with bovine serum albumin (Hagerman & Butler, 1978). Nitrogen, fibres, soluble phenols and tannins were analysed at the CIRAD laboratory ("Centre de Coopération Internationale en Recherches Agronomiques pour le Développement", Montpellier, France).

Data treatment

The decay rate coefficient (k) estimates the disappearance of leaf litter on a annual basis, using the negative exponential decay function $X_t/X_0=e^{-kt}$, where X_0 is the original amount of litter and X_t is the amount of litter remaining at time t (Olson, 1963). The k value was used to calculate turnover time (1/k) and the time required for 50% decomposition or the half-life of litter on the ground, $t_{1/2}$, calculated as 0.693/k.

Non-linear correlations (Spearman rank correlations) have been effected between final mass losses (at 14 months) of each species and initial concentrations or ratios of chemical constituents. Non-linear correlations were performed between final mass losses of each species and soil properties (% clays, % silts, soil water content, CEC, total C content, $\%P_2O_5$, % CaO and % K_2O). Non-linear correlations have been also effected between

initial concentrations or ratios of chemical constituents and mass loss of litter, over successive periods: 0-15 days, 15 days-1 month, 1-2.5 months, 2.5-5.5 months, 5.5-9 months, 9-12 months and 12-14 months.

Results

Soil of both forests had different physico-chemical characteristics. The secondary forest leptosol soil had a silt loam texture: 10% clay and 71% silt in surface layers; 49% clay and 28% silt in deeper layers. In the 10 upper cm, this soil was rich in organic matter (21% C) with a C:N ratio of 12.5. The organic matter content decreased in the deeper layers (8.8% C between 30 and 40 cm). The plantation vertisol had a clay texture: 78% clay in surface layers and 76% clay in deeper layers. In the upper 10 cm, this soil contained 5.3% C with a C:N ratio of 12. The soil organic matter content decreased in the deeper layers (1.2% C between 30 and 40 cm). In both soils, the water pH was higher than 7.5. Soil moisture (bi-monthly measurements) was not significantly different in the two forests. In the plantation vertisol, the water content was 21 ± 3% during the dry season and 45 ± 7% during the rain season. In the secondary forest leptosol, the water content was 18 ± 4% during the dry season and 43 ± 11% during the rain season. However, in this soil, the water content showed greater variations during the dry season with values which could be as low as 6%. During the dry season, the shallow leptosol was probably drier than the deeper vertisol, because it had not a sufficient stock of water to compensate for the lack of precipitation.

Chemical analyses (Table 1) showed that freshly fallen leaves of T. heterophylla had the lowest content in lignin, phenol and tannin. Due to the decrease in lignin content, these leaves were also characterised by the highest cellulose content (32% dry matter). Leaves of P. subcordata had a higher N content (2.5%) than all other species.

The percentage of leaf biomass remaining in the litterbags over the 14 month-period is

shown in Fig.1 and decomposition parameters are presented in Table 2. The initial mass loss was rapid (15 to 20% total mass loss during the first month), but the decomposition rate slowed down between 2.5 and 5.5 months (4 to 10% total mass loss over 3 months). After 14 months, 94% leaf biomass of T. heterophylla had disappeared as opposed to 57% for S. macrophylla, and 47% for B. simaruba in the forest plantation, 42% for P. subcordata and 38% for B. simaruba in the secondary forest. For the whole experimental period (after 14 months), a Kruskal Wallis non-parametric analysis of variance (followed by rank test) only showed a significant difference between decay rates of T. heterophylla and B. simaruba issued from the secondary forest ($p = 0.003$). Decay rate coefficients (k values) ranged from -0.41 to -0.46 in the secondary forest, and from -0.53 to -2.39 in the forest plantation (Table 2).

In the studied forests, neither litter chemical parameters nor soil properties were significantly correlated with decay rates when calculated over the whole experimental period by non-linear Spearman rank correlations. Nethertheless, several decomposition stages could be explained by a peculiar parameter of litter quality. Between 1 and 2.5 months, the mass loss was correlated negatively with the initial phenol content and with the initial lignin : N and (lignin + phenols) : N ratios (Table 3). At this stage, S. macrophylla that had the higher phenol content and the higher lignin : N and (lignin + phenols) : N ratios (Table 1) decomposed more slowly than other leaf species (Fig.1). Between 2.5 and 5.5 months, the mass loss was correlated negatively with the initial lignin content and positively with the initial cellulose content (Table 3). Leaves of T. heterophylla that are richer in cellulose and poorer in lignin (Table 1) decomposed more rapidly than other leaves. On the contrary, leaves of S. macrophylla and P. subcordata, richer in lignin and poorer in cellulose, decomposed more slowly (Fig.1). Between 9 and 14 months, the mass loss was correlated negatively with the initial tannin content. Leaves

of T. heterophylla that were poorer in tannin (0.3%) decomposed more rapidly than other leaves (Fig.1).

Discussion

In the semi-evergreen forests of Grande-Terre (Guadeloupe), decomposition rates (k ranged from -0.41 to -2.39) were within the range of other tropical forests with a relatively long dry season. The decomposition rates found in the secondary forest (k = -0.46 for P. subcordata and k = -0.41 for B. simaruba) ranged in the higher values. These decomposition rates were comparable with the high k values (from -0.39 to -0.61) found in secondary forests of Central Amazonia dominated by Cecropia species, particularly rich in tannins (Mesquita et al., 1998). On the contrary, the decomposition rates found in the plantation (k = -0.73 for S. macrophylla, k = -2.39 for T. heterophylla and k = -0.53 for B. simaruba) ranged in the low values, comparable to k values ranged from -1.1 to -2.3 found in Ethiopian highland forests (Lisanework & Michelsen, 1994).

Depending on stage of the decomposition process, different chemical parameters of litter correlated well with mass loss. Between 1 and 5.5 months, the mass loss was correlated negatively with the phenol and the lignin content of leaves and positively with their cellulose content. At this stage, after leaching of most soluble components, soil faunal activity becomes more important. Animals break up plant litter and mix it with mineral materials. During this stage, soil fauna probably neglect leaves with a higher content in phenol and lignin (Mangenot & Toutain, 1981; Harbone, 1997; Palm & Rowland, 1997), and thus their decomposition is slower. On the contrary, leaves with a high content in cellulose are preferred by soil invertebrates and disappear more rapidly. Lignin and phenols are degradable only by a few organisms, contrary to cellulose (Kirk, 1983 Harbone, 1997; Palm & Rowland, 1997). Cellulose has an intermediate quality and can be

used as an energy source by several decomposers. It is a major component of the foliage and we believe it should be included in the plant quality minimum dataset (beside N, lignin, soluble C, ash-free dry weight, total P and soluble phenolics), as defined by Palm & Rowland (1997). In the late phase of decomposition (9-14 months), decomposition rates were correlated with the initial tannin content. Leaves initially richer in tannins decomposed more slowly than other leaves in the long term. Tannins generally combine with protein (tannin-protein complexes), decreasing the protein degradation rate (Davies et al., 1964). The initial tannin content of leaves could be an important chemical parameter for predicting long-term decomposition rates.

In our study, we observed two main periods in the decomposition process: an initial phase, that lasted 1 month, corresponding probably to the elimination of initial hydrosoluble compounds, and a late phase, with a decreased decomposition rate. In other studies, the initial mass loss has been shown to be due to the leaching of soluble C initially present and to a high microbial activity based on the most easily degradable compounds such as sugars and amino-acids (Palm & Rowland, 1997). During late stages, decomposition rates were influenced negatively by slowly degradable compounds (lignin, phenols, tannins) and positively by more degradable compounds (cellulose). However, the behaviour of T. heterophylla leaves was different in that its decomposition rate seemed to be rather constant (see Fig.1). The better chemical quality of T. heterophylla leaves, i.e., their lower lignin and tannin content (12% and 0.3% dry matter, respectively), and the correspondingly higher cellulose content (32% dry matter) probably explains why the decomposition rate does not drop down after the initial phase.

The present study supports the contentions that litter quality was one of the most important determinant of decomposition in tropical forests (Lavelle et al., 1993). It also supports the contention that mass loss must be correlated with litter chemical parameters at

different stages of litter decomposition for a better understanding of decomposition dynamics. Finally, this study suggests that it is necessary to include tannins and cellulose in the minimum dataset characterising of plant quality, at least for tropical forest tree species.

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Table 1 Initial quality parameters and ratios of chemical constituents (means ± S.E.) of leaves incubated in litterbags during a 14 months period, in the secondary forest and in the forest plantation (Grande-Terre, Guadeloupe). Bags filled with P. subcordata and B. simaruba leaves were placed in the secondary forest; bags filled with S. macrophylla, T. heterophylla and B. simaruba leaves were placed in the plantation. n = 3

	P. subcordata	S. macrophylla	T. heterophylla	B. simaruba
Total N (%)	2.5 ± 0.1	1.1 ± 0.1	0.9 ± 0.1	1.1 ± 0.1
Soluble C (%)	2.4 ± 0.5	3.0 ± 0.3	5.3 ± 0.3	8.3 ± 0.3
Cellulose (%)	19.2 ± 0.6	19.8 ± 4.1	32.1 ± 2.3	20.9 ± 0.4
Lignin (%)	29.5 ± 15.1	29.1 ±10.0	12.0 ± 2.1	22.8 ± 9.6
Soluble phenols (%)	6.7 ± 0.6	12.7 ± 0.6	4.5 ± 2.3	10.0 ± 1.0
Tannins (%)	1.8 ± 0.8	2.9 ± 0.6	0.3 ± 0.1	3.3 ± 0.7
Lignin : N	11.7 ± 1.1	26.5 ± 0.9	13.5 ± 0.3	20.7 ± 0.8
(Lignin + Phenols) : N	14.3 ± 1.6	38.0 ± 1.0	18.5 ± 0.5	29.8 ± 1.1

Table 2 In situ decomposition parameters for four litter species from the secondary forest and the forest plantation (Grande-Terre, Guadeloupe). The decomposition constant k was calculated from $(X_t/X_0)= e^{-kt}$; R^2= correlation coefficients; half-life ($t_{1/2}$)= 0.693/k; turnover= 1/k. n= 4 litterbags for each species and for each 7 collection date; t = 14 months.

	P. subcordata (secondary forest)	B. simaruba (secondary forest)	S. macrophylla (forest plantation)	T. heterophylla (forest plantation)	B. simaruba (forest plantation)
k	-0.46	-0.41	-0.73	-2.39	-0.53
R^2	0.96	0.93	0.94	0.90	0.94
half-life (months)	18	20	11	4	16
turn-over (months)	26	29	17	5	23

Table 3 Spearman rank correlation coefficients (r) between mean mass losses of leaf litter (during successive periods) and initial concentrations or ratios of chemical constituents in the secondary forest and in the forest plantation (Grande-Terre, Guadeloupe). Bags filled with P. subcordata and B. simaruba leaves were placed in the secondary forest; bags filled with S. macrophylla, T. heterophylla and B. simaruba leaves were placed in the plantation. n = 5. Significant values at P = 0.05 are in bold type.

	0 - 15 days	15 days - 1 month	1 - 2.5 months	2.5 - 5.5 months	5.5 - 9 months	9 - 12 months	12 - 14 months
Soluble C (%)	r = 0.36	r = 0.72	r = -0.15	r = 0.56	r = -0.21	r = -0.56	r = -0.56
Lignin (%)	r = - 0.46	r = - 0.72	r = -0.36	**r = -0.93**	r = -0.41	r = -0.15	r = -0.15
Cellulose (%)	r = 0.46	r = 0.72	r = 0.36	**r = 0.93**	r = 0.41	r = 0.15	r = 0.15
Soluble phenols (%)	r = -0.56	r = -0.41	**r = -0.98**	r = -0.67	r = -0.21	r = -0.36	r = -0.36
Tannins (%)	r = -0.05	r = 0.21	r = -0.67	r = -0.15	r = -0.62	**r = -0.93**	**r = -0.93**
N (%)	r = -0.56	r = -0.72	r = -0.21	r = -0.83	r = -0.67	r = -0.21	r = -0.36
Lignin : N	r = -0.30	r = -0.10	**r = -0.90**	r = -0.30	r = 0.20	r = -0.20	r = -0.10
(Lignin + Phenols) : N	r = -0.30	r = -0.10	**r = -0.90**	r = -0.30	r = 0.20	r = -0.20	r = -0.10

Figure captions

Fig. 1 Percent remaining dry biomass of four leaf litter types incubated over 14 months in the forest floor of a secondary forest and a forest plantation (Grande-Terre, Guadeloupe). Bags filled with P. subcordata and B. simaruba leaves were placed in the secondary forest; bags filled with S. macrophylla, T. heterophylla and B. simaruba leaves were placed in the plantation. Points are means of four litterbags retrieved at each time interval; bars represent +/- 1 SE.

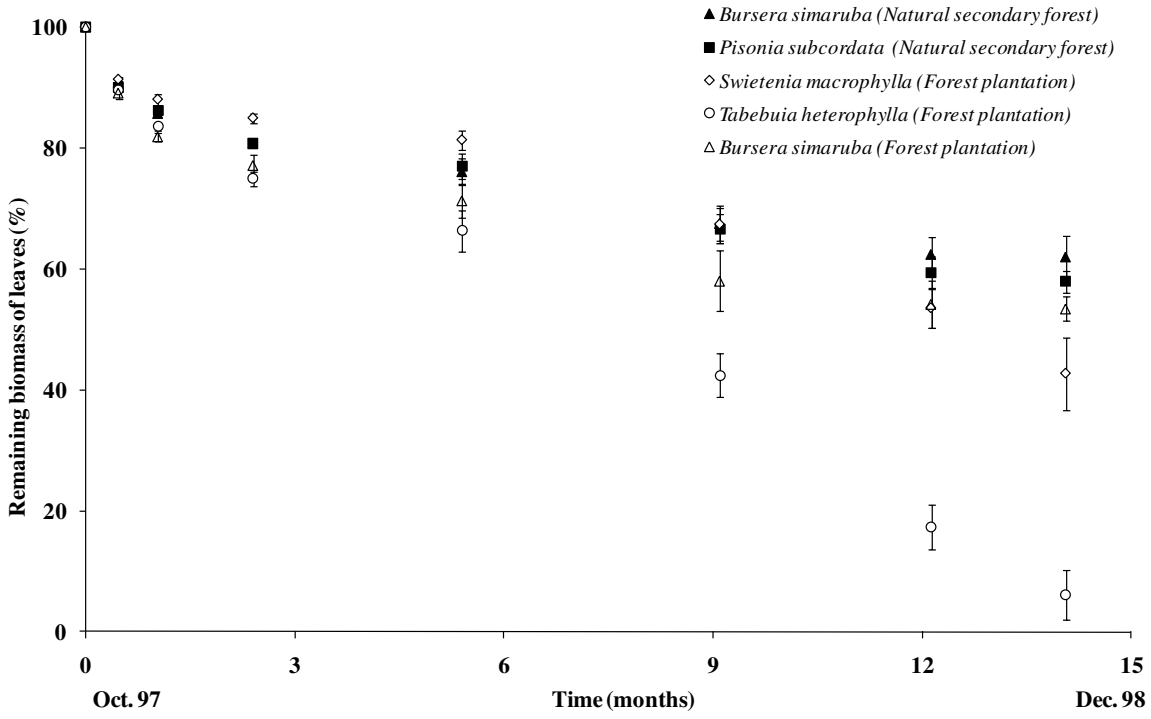
▲ Bursera simaruba (Natural secondary forest)
■ Pisonia subcordata (Natural secondary forest)
◇ Swietenia macrophylla (Forest plantation)
○ Tabebuia heterophylla (Forest plantation)
△ Bursera simaruba (Forest plantation)
Remaining biomass of leaves (%)
100
80
60
40
20
0
0
3
6
9
12
15
Oct. 97
Time (months)
Dec. 98

Fig. 1