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Leaf litter decomposition in tropical rainforest of Ebom, Southwest Cameroon: comparison among guild classes

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Abstract: Decomposition processes of guild classes - groups of plant species with a similar ecology and way of life in the tropical rainforest are poorly understood. Leaf litter decomposition and nutrient dynamics of the following three guild classes were studied in the tropical rainforest of Ebom, Southwest Cameroon: the shade tolerant (ST), non-pioneer light demanding (NP) and pioneer (PI) species. The litterbag technique was used to assess mass loss and decay rate. During the 23 weeks of the field experiment, mean dry mass remaining of litter samples with standard error was between 29.16 ± 18.17 and 60.19 ± 18.81 % of initial litter dry mass for ST and PI, respectively. Decomposition rate constant (k) significantly ranged from 0.02 (PI) to 0.08 % week^{-1} (ST). Initial nutrient contents widely varied among guild classes and revealed low nutrient contents in pioneer species and high contents in the other groups, except for Ca. Mean nutrient release from initial contents was significantly 50.62 % and 85.11 % respectively for N and Ca in ST; it varied significantly from 80.68 (NP) to 95.13 % (PI) for K and no significant nutrient releases were observed for Mg, Na and P. Thus, while litter decomposition was significantly influenced by guild classes, nutrient loss, with the exception of K, was not, and this should be explained by the short term of litter decomposition.

Resumen: El entendimiento de los procesos de descomposición de clases de gremios - grupos de especies vegetales con ecología y maneras de vivir similares - en el bosque tropical húmedo es pobre. Se estudió la descomposición de especies y la dinámica de nutrientes de las siguientes tres clases de gremios en el bosque tropical húmedo de Ebom, suroeste de Camerún: especies tolerantes a la sombra (ST), especies no pioneras demandantes de luz (NP) y especies pioneras (PI; siglas en inglés). Se usó la técnica de la bolsa de mantillo para evaluar la pérdida de masa y la tasa de descomposición. Durante las 23 semanas del experimento de campo, la masa media remanente de las muestras de mantillo (con error estándar) fluctuó entre 29.16±18.17 y 60.19±18.81 % de la masa seca inicial de mantillo para ST y PI, respectivamente. La constante de la tasa de descomposición (k) varió significativamente de 0.02 (PI) a 0.08 % semana^{-1} (ST). Los contenidos iniciales de nutrientes variaron ampliamente entre las clases de gremios y revelaron contenidos bajos de nutrientes en las especies pioneras y contenidos altos en los otros grupos, excepto de Ca. La liberación media de nutrientes de los contenidos iniciales fue significativamente diferente, 50.62 % y 85.11 %, respectivamente, para N y Ca en ST; varió significativamente de 80.68 (NP) a 95.13 % (PI) para K y no se observaron liberaciones significativas de Mg, Na y P. Por lo tanto, mientras que la descomposición del mantillo estuvo influenciada significativamente por las clases de gremios, la pérdida de nutrientes (con excepción de K) no lo estuvo, y esto debiera ser explicado por la descomposición de mantillo de corto plazo.

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Resumo: Os processos de decomposição por classes de qualidade - grupos de espécies de plantas com uma ecologia e modo de vida semelhantes - na floresta tropical húmida são mal compreendidos. As dinâmicas da decomposição da folhada e a dos nutrientes das seguintes três classes de qualidade foram estudados na floresta tropical húmida de Ebom, no sudoeste dos Camarões: a classe das espécies tolerantes à sombra (ST), a de espécies de luz não pioneiras (NP) e espécies pioneiras (PI). A técnica de uso dos sacos foi utilizada para avaliar a perda de massa e taxa de decomposição. Durante as 23 semanas da experimentação de campo, a massa seca média de folhada remanescente nos sacos, com o respectivo erro padrão, variou entre 29,16 ± 18,17 e 60,19 ± 18,81 % da massa seca inicial da folhada para ST e PI, respectivamente. A taxa constante de decomposição (k) variou significativamente de 0,02 (PI) para 0,08 % semana^{-1} (ST). O teor inicial de nutrientes variou amplamente entre as classes de qualidade e revelou baixos teores de nutrientes nas espécies pioneiras e teores altos nos outros grupos, excepto para o Ca. A média de libertação de nutrientes em relação aos teores iniciais foi significativa, atingindo valores de 50,62 % e 85,11 %, respectivamente para N e Ca em ST; variou significativamente de 80,68 (NP) para 95,13 % (PI) em relação ao K. Contudo, a libertação observada de nutrientes não foi significativa para o Mg, Na e P. Assim, enquanto decomposição foi significativamente influenciada pelas classes de qualidade, a perda de nutrientes, com exceção do K, não foi observada, e isso deve ser explicado pelo curto período de estudo da decom-posição.

Key words: Litter decomposition, nutrient dynamics, tropical rainforest of Ebom.

Introduction

In forest ecosystems, more than 90 % of net aboveground primary production returns to the forest floor as litterfall which constitutes the major substrate for plant species and soil decomposers (Swift *et al.* 1979). Litter decomposition includes leaching, breakdown by soil fauna, and transformation of organic matter by microorganisms and transfer of organic compounds and nutrients to the soil. This process is mostly biological, but is influenced by abiotic factors through their effects on soil fauna. Climate, soil characteristics, resource quality, and soil organisms are the most important factors regulating litter decomposition (Brouwer 1996; Gillon *et al.* 1994; Swift *et al.* 1979; Trofymow *et al.* 2002). However, in some climatic regions, and particularly in the tropics, litter quality parameters seem to be the best predictors of decomposition rates, whereas environmental conditions such as soil characteristics and micro-climate tend to be less important (Lavelle *et al.* 1993; Meentemeyer 1978). Information on litter decomposition in lowland tropical rainforests is also relatively poor compared to that of temperate forests (Hirobe *et al.* 2004).

The impact of plant species on litter decomposition and nutrient availability depend on the chemical composition of their litterfall, tree species and species groups such as climax and pioneers (Brouwer 1996; Mesquita *et al.* 1998; van Dam 2001). These aspects are particularly prominent in lowland tropical rainforest because of the mosaic of vegetation development phases and high species diversity (Swift & Anderson 1989). But the relationships between tree species composition, tree categories or groups and litter decomposition are not clear in tropical rainforest because of the heterogeneity of vegetation (Madge 1965; Proctor *et al.* 1983) and a lack of existing studies.

Three guild classes, each guild circumscribing a group of plant species with a similar ecology and way of life (Hawthorne 1996), characterize the tropical rainforests: (1) pioneer species that colonize the forest gaps after disturbance, (2) the non-pioneer light-demanding species that need sunlight for growth in their juvenile stage, (3) shadow-bearing or shade tolerant species at a mature state or climax species developing under low sunlight conditions. Existing results on litter decomposition rate and nutrient release vary accordingly amongst studies and the type of forests studied (Brouwer 1996; Mesquita *et al.* 1998; van Dam 2001). Thus far, no study has been conducted to compare the litter decomposition process among non-pioneer light demanding and shade-bearer species in Ebom forest. Hence, the objective in this study was to compare patterns of litter decomposition and nutrient release in three guild classes with contrasting litterfall chemical composition in the tropical rainforest of Ebom, South-west Cameroon.

Materials and methods

Study site

The experiment was conducted in Ebom undisturbed forest, within the Tropenbos Cameroon Programme (TCP) research area, which is located in the western portion of the Atlantic Biafran forest of south Cameroon, lying within the Congo-Guinea refuge. The experimental site is located at 3º 05' N and 10º 41' E, with elevation of ~440 m. The bedrock is composed of Precambrian metamorphic as well as old volcanic rocks (Franqueville 1973). The soil is clay-rich (35-70 %) and strongly acidic (van Gemerden & Hazeu 1999). The climate is humid tropical with four seasons: a long (mid-November to mid-March) and short (mid-May to mid-August) dry season, and a long (mid-August to mid-November) and short (mid-March to mid-May) rainy season. Mean annual rainfall is about 2100 mm and mean annual temperature is 22.9 °C (van Gemerden & Hazeu 1999). The portion of forest selected for the experiment was characterized by the absence of recent natural or human disturbance. Relevant characteristics of this site like location, rainfall data and soil physio-chemical characteristics are presented in Table 1. Vegetation consists of evergreen forest rich in Caesalpiniaceae species (Letouzey 1985), characterised by tall trees that reach heights of about 60 m. Tree density was about 521 trees per hectare, basal area of about 29.84 m^2 ha^{-1} and diameter classes ranged from 9.39 to 150 cm, with a mean of 21.34 cm (Ibrahima *et al.* 2002). At some places in the forest Bantou people practice shifting agriculture with short fallows (Nounamou & Yemefack 2001), while Banyeli Pygmy people live from gathering and hunting. Many non-timber forest products like bushmeat, honey, mushrooms, fruits, leaves, seeds and roots are harvested (van Dijk 1999).

Leaf litter selection

In this study, only freshly-fallen leaf litter was used. The experiment involved three guild classes (Table 2): Three shade tolerant (ST) trees, which grow, flower and fruit in undisturbed forest (*Plagiostyles africana*, *Strombosia scheffleri* and *Vitex grandifolia*), three non-pioneer light deman-ding (NP) (*Guibourtia tessmannii, Klainedoxa gabonensis* and *Pterocarpus soyauxii*) and two pioneer (PI) tree species (*Musanga cecropioides* and *Xylopia aethiopica*). Litter samples were colle-cted fortnightly, except in the long rainy season where litter was collected at weekly intervals from twenty litter traps. The litter samples were taken to the laboratory in polythene bags and dried. The samples of each month were bulked and categorized into leaf, wood and all remaining material. Only leaf litter was used for the decomposition experiment. The leaf litter was sorted by species.

Table 1. Characteristics of the Ebom rain forest*.

Variable	Data
Location	3° 05' N, 10° 41' E
Elevation (m a.s.l.)	440
Rainfall (mm)**	2115.3
Relief intensity (m)	moderate (30-80)
River density	Moderate
Vegetation	lowland forest
Soil types	Ultisols / Oxisols (infertile)
Clayey (topsoil, 0-10 cm) (%)	20-50 (clay)
Sandy (%)***	40-60
pH (water)***	4.7
Carbon (%)***	4-8
Nitrogen (%)***	0.25-0.50
C/N	10
Available P (ppm)	12-26
Total P (ppm)***	150-400
K (meq/100g of soil)***	0.1-0.9
Mg (meq/100g of soil)***	0.4-1.6
Ca (meq/100g of soil)***	0.5-4
Al (meq/100g of soil)***	0.5-6

* Source: van Gemerden and Hazeu (1999).
** Annual mean of rainfall collected from 1996 to 2000.
*** Top soil (0-10 cm depth).

Decomposition experiment

A litterbag experiment was carried out to compare leaf decomposition rates of the three guild classes. Litterbags used in this study consisted of nylon material with a 2 mm mesh (Brouwer 1996; Swift *et al.* 1979). The bags were of different sizes according to litter type to avoid compressing the

Table 2. Species consisting of guild classes: shade tolerant (ST), non-pioneer light demanding (NP) and pioneer (PI) in Ebom rainforest.

Family name	Species name	Guild classes
Euphorbiaceae	*Plagiostyles africana* (Mull. Arg.) Prain,	ST
Olacaceae	*Strombosia scheffleri* Engl.	ST
Verbenaceae	*Vitex grandifolia* Gurke	ST
Caesalpiniaceae	*Guibourtia tessmannii* (Harms) J. Loenard	NP
Caesalpiniaceae	*Klainedoxa gabonensis* Pierre ex. Engl.	NP
Fabaceae	*Pterocarpus soyauxii* Taub	NP
Cecropiaceae	*Musanga cecropioides* R. Brown ex. Tedlie	PI
Annonaceae	*Xylopia aethiopica* (Dunal) A. Rich	PI

material and thus creating artificial conditions in the litterbags. The choice of the litterbags and mesh sizes was based on other studies of litter decomposition (Ibrahima 1995; Swift & Anderson 1989). In total, 144 litterbags (6 sampling dates x 3 replications x 8 species) were each filled with 5 ± 0.01 g of the leaf litter and placed on top soil, from 18 January to 29 June 2001. Three litterbags per species were collected at 2, 4, 6, 9, 14 and 23 week intervals, brought to the laboratory where all roots, fauna, and soil particles were manually removed from the litter. The dry mass of the samples in each litterbag was determined after it was oven-dried at 60 °C to constant mass. To dete-rmine initial dry mass and nutrient content, three other litter samples of each species not including in the above mentioned (144 samples) were weighed and dried at 60 °C to constant mass. The dry mass remaining of species of each guild class was calculated.

Chemical analysis

The samples were ground into a powder and then mineralised by passing the powder through a furnace at 550 °C for 40 min. The ashes were re-collected with a diluted HNO_3 solution for nutrient analysis: Ca and Mg were determined with an atomic absorption spectrophotometer; K and Na with a flame spectrophotometer; P with a vanado-molybdate colorimeter. N analysis was done by the Kjeldahl method and its titration by sulphuric acid at 0.01N. Carbon content was determined by the colometrical method (Okalebo *et al.* 1993).

Statistical analysis

Decomposition rate constants (k) were estimated using the simple negative exponential decay function (Olson 1963): $DMR = 100e^{-kt}$, where DMR is the litter dry mass remaining and t is time of decomposition. This model is widely used and enables easy comparison with other studies.

The nutrient content remaining as a percentage of the initial quantity was calculated from the following equation (Bockheim *et al.* 1991): $QR = (C/C_0)*(DM_t/DM_0)*100$, where QR is the nutrient content remaining (%); C and C_0, are respectively nutrient content at time t and t_0 or initial time; DM_t and DM_0 are dry mass at time t and t_0.

Before performing any analysis, all variables were tested for normality and if necessary, log transformed. The comparison of dry mass remaining (DMR) at each sampling date, as well as the nutrients remaining among guild classes was carried out by using ANOVA, followed by *Scheffe*'s test at $P < 0.05$, if ANOVA was significant. A multiple comparison among the fitted de composition constants (k) was carried out using the *T'-method* (Sokal and Rohlf 1981).

Nutrient content at the last incubation (23 weeks after incubation) was compared to those measured in the initial litter for each guild class (Student t test). The loss of nutrients was calculated as the difference between the initial absolute amount and the final one of each nutrient and the same difference was also expressed as a percentage of the initial amount (%) if the *Student t* test was significant. These tests were conducted through software package SX for DOS, version 4.0. (Statistix 1992).

Results

Dry mass remaining

The dynamics of mass loss was fastest at the beginning of the litter decomposition experiment and slowed over time, except for the pioneer species (Fig. 1). At the each sampling date, the dry mass remaining differed significantly between the guild classes except for the first sampling date. At the end of litter incubation in litterbags *in situ*, the dry mass remaining varied significantly (F = 4.85; $P < 0.05$) from 29.16 to 60.19 % of initial dry mass for pioneer and shade tolerant species, respectively (Fig. 1). Thus, the corresponding mass loss was between 70.84 and 39.81 %. In general, the litter decomposition of PI species was significantly lower than that of ST and NP, which did not differ significantly between them.

The coefficients of determination of the litter decomposition constants (k) were all highly significant ($P < 0.001$). Their mean values varied significantly from 0.018 for pioneer species to 0.081 week^{-1} for ST species (Fig. 2), suggesting that the litter decomposition rate was fast, slow and intermediate in ST, PI and NP species, respectively. But, only PI was significantly lower ($P < 0.05$) than the two other groups, which were both considered as climax species.

Nutrient dynamics in decomposing litter

Initial nutrient contents varied among guild classes (Table 3). Differences between the three groups were only significant for Mg and K. The litters of ST species were richer in Mg than PN and PI species. Initial content of K of NP litter was significantly greater than that of PI litter.

After 23 weeks of litter incubation *in situ*, release of nutrients varied according to nutrient and guild classes (Table 4). N and Ca were significantly released from only ST litter, with respective rate contents of 50.62 and 85.11 % of the initial contents. Mg and P were not significantly released or gained from any of the three guild classes. Conversely, K was the only nutrient that was significantly released by the litters of all three guild classes. This loss varied from 14.98 mg in NP to 27.91 mg in PI species, with corresponding rate of 80.68 and 95.13 %, respectively. Na continued to be immobilized in the litter after 23 weeks of litter incubation for all three guild classes, but this immobilization was significant in only NP litter, which had an immobilization rate of 202 %. ST litter significantly released N, Ca, and K compared to the initial values at 23 weeks after incubation *in situ*, with the rate reaching respectively 50.62, 85.11 and 92.30 % of the initial contents (Table 4). NP and PI litter significantly released only K, with respective rates of 80.68 and 95.13 % of initial contents. Across all guild classes nutrient release could be classified as follows: K (89.04 %) > Ca (60.80 %) > Mg (46.19 %) > N (40.99 %) > P (24.17 %).

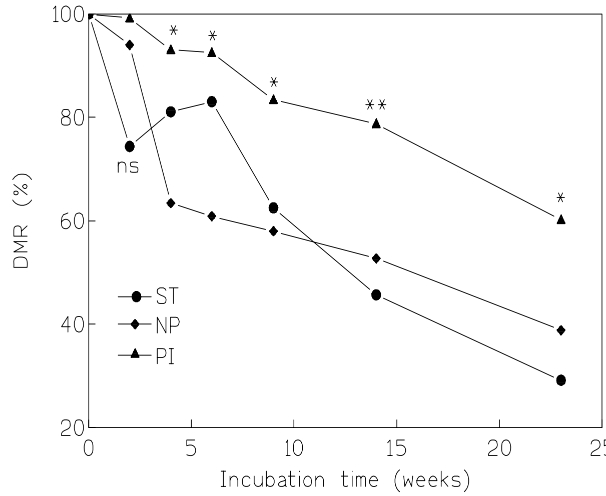

Fig. 1. Litter dry mass remaining (DMR) of three guild classes (ST, NP and PI) during the course of the incubation in the Ebom rainforest of Southwestern Cameroon.

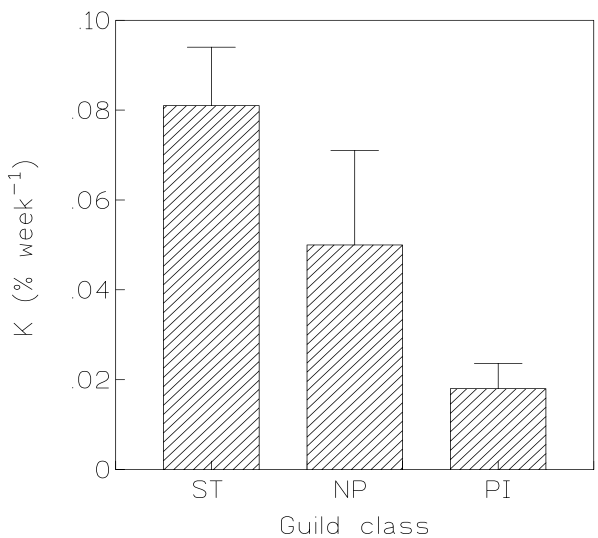

Fig. 2. Litter decomposition rate constants (k in % week^{-1}) of three guild classes in the Ebom rainforest of Southwestern Cameroon.

Discussion and conclusion

We could find no existing studies comparing litter decomposition process of three guild classes like shade tolerant, non-pioneer light-demanding and pioneer tree species in the literature. However, some results on litter decomposition of climax and pioneer tree species were reported. Brouwer (1996) has shown that the decomposition rate of the litter of pioneer species can be much faster than that of a climax species like *Chlorocardium rodiei* in tropical forest of Guyana. van Dam (unpublished data), cited by van Dam (2001) observed that leaves of another pioneer species *Goupia glabra* were almost completely decomposed after 1 year, while the firm leaves of the climax species *C. rodiei* had only 52 % of mass loss after 1 year. These two experiments were conducted in forest gaps. This fast decomposition rate of pioneer leaf litter was attributed to its high nutrient content and degradability (Dantas & Phillipson 1989). However, our results have shown that leaf litter decomposition of climax species (ST and NP) was significantly faster than that of pioneer species (PI) and confirm those reported by Mesquita *et al.* (1998), who found slower litter decomposition of pioneer species (*Cecropia sciadophylla*) compared to those of climax species in Amazonian tropical forest.

Table 3. Mean values of nutrient content (g kg^{-1}) in initial litter of three guild classes: shade tolerant (ST), non pioneer light demanding (NP) and pioneer (PI) in Ebom rainforest. Standard deviation in parenthesis.

	Guild classes			
Nutrient	ST	NP	PI	Fisher F
C	540.00 (101.00)	477.50 (185.96)	470.00 (70.71)	0.26ns
N	20.68 (8.00)	13.33 (3.24)	11.41 (1.19)	2.46ns
C/N	28.50 (11.10)	43.49 (11.23)	41.74 (10.55)	2.05ns
Ca	2.50 (1.63)	1.75 (0.80)	2.28 (0.63)	0.39ns
Mg	0.77 (0.17) a	0.39 (0.18) b	0.16 (0.13) b	10.07**
K	4.81 (1.96) ab	6.35 (1.95) a	1.39 (0.71) b	4.91*
Na	0.011 (0.009)	0.006 (0.001)	0.005 (0.001)	0.85ns
P	0.56 (0.12)	0.62 (0.12)	0.37 (0.04)	3.09ns

* $P < 0.05$; ** $P < 0.01$; ns: not significant. Different letters in the same row indicate that values are significantly different.

Table 4. Mean differences in nutrient amounts between the initial litter and that obtained after 23 weeks of incubation, expressed in mg and, if these differences were significant, as a percentage of the initial quantity.

Nutrient		Guild classes		
		ST	NP	PI
N	Initial amount	53.77 (10.95)	65.48 (11.49)	58.48 (28.19)
	Final amount	26.56 (14.07)	47.50 (16.50)	27.15 (15.95)
	Student t	3.05*	1.79ns	1.37ns
	+/- (mg)	-27.22	-17.98	-31.33
	%	50.62		
Ca	Initial amount	9.19 (2.78)	11.16 (3.31)	4.25 (1.67)
	Final amount	1.37 (1.44)	6.62 (7.60)	1.65 (1.32)
	Student t	4.99**	1.10ns	1.72ns
	+/- (mg)	-7.82	-4.56	-2.60
	%	85.11		
Mg	Initial amount	2.24 (1.79)	2.09 (1.53)	1.88 (0.34)
	Final amount	1.06 (0.78)	1.54 (1.06)	0.48 (0.42)
	Student t	1.21ns	0.60ns	3.69ns
	+/- (mg)	-1.19	-0.56	-1.41
	%			
K	Initial amount	20.18 (11.96)	18.57 (7.33)	29.34 (7.99)
	Final amount	1.55 (1.03)	3.59 (1.44)	1.43 (0.96)
	Student t	3.10*	4.01*	4.90*
	+/- (mg)	-18.62	-14.98	-27.91
	%	92.30	80.68	95.13

Contd...

Table 4. Continued.

Nutrient		Guild classes		
		ST	NP	PI
Na	Initial amount	0.05 (0.05)	0.03 (0.01)	0.02 (0.01)
	Final amount	0.32 (0.58)	0.08 (0.02)	0.05 (0.04)
	Student t	0.91ns	5.00**	0.91ns
	+/- (mg)	+0.26	+0.05	+0.03
	%		202.00	
P	Initial amount	2.29 (0.61)	2.48 (0.73)	3.08 (0.47)
	Final amount	1.51 (0.66)	2.55 (1.24)	1.45 (0.57)
	Student t	1.75ns	0.10ns	3.14ns
	+/- (mg)	-0.79	+0.08	-1.63
	%			

Shade tolerant (ST), non-pioneer light demanding (NP) and pioneer (PI) species. Nutrient loss (-) or gain (+) in mg and percentage when *t* of student is significant. * $P < 0.05$, ** $P < 0.01$ and ns: not significant.

The differences between our results and those of Brouwer (1996) and van Dam (2001) can be explained by the fact that their experiments were carried out in large gaps with a preponderance of PI species, while our experiments were conducted in undisturbed forest. In addition, the PI species observed in the two experiments were different: *Cecropia sciadophylla* and *Goupia glabra* vs *Musanga cecropioides* and *Xilopia aethiopica.* Nutrient contents, particularly Mg and K, were also lower in PI species.

Among the guild classes, within the 23 weeks of litter incubation, the average mass loss and the litter decomposition rate constants of ST species (70.84 % and 0.081 week^{-1}) were the highest, those of PI species (39.81 % and 0.018 week^{-1}) were the lowest, and those of NP species (61.16 % and 0.05 week^{-1}) were intermediate. But the values of ST and NP groups, considered as climax, overlapped and were not significantly different. This indicates that litter decomposition was not effected by climax species. In fact, after 23 weeks of incu-bation, more than 60 % of litter mass loss occurred in both groups.

The initial nutrient contents of litters differed among guild classes, but these differences were non-significant except for Mg and K. The initial content of Mg decreased from ST to PI species. This nutrient could not only partly explain the differences in litter decomposition between the guild classes, but it could also play a limiting role in litter decomposition in the Ebom rainforest. In fact, some studies suggest that low initial nutrient/N ratios (< 0.05) are indicative of nutrient limitations in ecosystems (Medina *et al.* 1990). It was observed in this study that mean values of Mg/N ratio was lower than 0.05, with the ratios of 0.04, 0.03 and 0.01, respectively for ST, PN and PI.

It can be inferred from this study that litter decomposition in the tropical rainforest of Ebom was the highest in ST species, lowest in PI species and intermediate in NP species after 23 weeks of litter incubation. However, only PI species was significantly different from the two other classes in litter decomposition. These results were in agreement with those of the literature. Conversely, the release rate of nutrients 23 weeks after litter incubation *in situ* were not clearly different among guild classes and revealed that the patterns of nutrient release are complex in the tropical rainforest of Ebom.

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