

## Litter fall, litter stocks and decomposition rates in rainforest and agroforestry sites in central Amazonia

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### Abstract

The sustainability of agroforestry systems in Amazonia was assessed from their litter dynamics and decomposition. Litter fall and litter stocks were determined from July 1997 to March 1999 in four sites in central Amazonia: a primary rainforest, a 13-year-old secondary forest, and two sites of a polyculture forestry system which consisted of four planted tree species of commercial use amidst upcoming secondary growth. The average annual litter fall in the undisturbed primary rainforest (FLO) was  $8.4 \text{ t ha}^{-1} \text{ year}^{-1}$ , which is within the range of litter fall in other rainforests in the region. It was similar in one of the two polyculture sites ( $8.3 \text{ t ha}^{-1} \text{ year}^{-1}$ ), but lower in the secondary forest and in the second polyculture site. In the litter fall in secondary forest and agroforestry sites, the leaf portion was higher (76–82% of total litter fall) than in FLO, due to reduced fine matter and wood fall. Leaf litter fall variability was much lower in the plantation sites than in the forests, which is explained by the much more homogeneous stand structure of the plantations. The quality of the produced litter, measured as C/N ratio, differed significantly between the primary forest site and one polyculture and the secondary forest site. The cumulative input of nitrogen through litter fall was  $144 \text{ kg ha}^{-1} \text{ year}^{-1}$  in FLO, and  $91\text{--}112 \text{ kg ha}^{-1} \text{ year}^{-1}$  in the polycultures and the secondary forest. Litter fall was not correlated with soil parameters, but had a significant linear regression with canopy closure. For the primary rainforest, litter fall was also (inversely) correlated with monthly rainfall. Litter fall was higher in the first year (1997–1998; an El Niño period) than in 1998–1999. Litter stocks on the forest floor were highest in the secondary forest ( $24.7 \text{ t ha}^{-1}$ ), and much lower in the polyculture sites ( $15.1\text{--}16.2 \text{ t ha}^{-1}$ ) and the primary forest ( $12.0 \text{ t ha}^{-1}$ ). There were no differences in the relative N content (C/N ratio) of the litter stocks between the sites, but the larger stocks led to higher absolute N contents in the litter layer in the secondary forest. From the monthly values of litter stocks (S) and litter fall (P), the decomposition coefficient  $k_e = P/S$  was calculated, which was, on average, highest for the primary forest (0.059), followed by the polyculture systems (0.040–0.042), and by the secondary forest (0.024). Thus, due to low decomposition rates, the secondary forest site showed large litter accumulations in spite of a relatively low litter fall. In contrast, the primary forest showed high litter fall but low stocks, due to high decomposition rates. The decomposition coefficients of the polyculture systems ranged between the primary and the secondary forest. The reduced decomposition rates in the man-managed agroecosystems indicate quantitative and/or qualitative changes in the decomposer communities of these systems that lead to a higher build-up of litter stocks on the forest floor. However, the decomposer systems in the polyculture sites still were more functional than in the site of non-managed secondary growth. Thus, from a soil biological viewpoint, ecologically sustainable low-input agroforestry in Amazonia will benefit from the application of these polyculture systems.

## Introduction

The tropical rainforest ecosystem in central Amazonia (Gentry 1990) is known for its low resilience to disturbance; its transformation into conventional agroecosystems based on annual crops or pasture is problem-ridden (e.g., Anderson 1990) and leads to soil degradation (Hölscher et al. 1996; Kato 1998). Therefore, the creation of persistent, sustainable agroforestry systems is imperative (Nair 1993; Young 1997). These systems should mimic rainforest features, such as high plant and decomposer diversity, closed forest canopy or closed surface cover (Martius et al. 2004a), to maximize their ecological function. Litter is a central nutrient resource in tropical forest ecosystems where soils are highly weathered and nutrient-poor; litter initiates the nutrient cycles by providing input to the decomposer food chain. Determining the dynamics of litter fall and available litter stocks over time is therefore a central task in studies of terrestrial ecosystem functions. Here we report on litter dynamics in a primary rainforest, a secondary forest (13 years old), and two experimental agroforestry plantation sites, as part of a study on the structure and dynamics of the decomposition processes in agroforestry systems in central Amazonia (Beck et al. 1998a,b; Höfer et al. 2000).

Decomposition rates are an indicator of the functionality of the biogenic below-ground ecosystem processes of nutrient cycling that include litter decomposition and nutrient supply and in which soil organisms play a central role (Tian et al. 1997; Lavelle et al. 1997, 2001; Rees et al. 2001; Tian and Badejo 2001). Biodiversity of soil organisms measurably affects the long-term soil fertility (Mäder et al. 2002). Vlek et al. (1997) have called for an improved recycling of soil nutrients to maintain the nutrient balance in agriculturally managed tropical soils, and become less dependent on external inputs.

Litter dynamics is governed by litter fall on one side, and the decomposition of the litter on the other. Decomposition rates can therefore be determined on the basis of litter stocks and litter fall. This goes back to Olson (1963), who postulated that in a steady state ecosystem the decomposition of the litter found on the forest floor (the stock  $S$ ) must be in equilibrium with the production rate of the litter (the litter fall or production  $P$ ). Therefore, the product  $P/S$  gives an indication of the decomposition rate at which the stocks are depleted. Mature rainforests can be seen as being in a steady state, but obviously this assumption

does not apply to early successional stages like secondary forest or young plantations like those considered in the present study. Nevertheless, the ratio  $P/S$  should allow to calculate the decomposition in all input–output systems in which both parameters are determined over a comparable period of time  $\Delta t$ . We expected the decomposition rate in young successional systems to be low, because little litter is produced and the decomposer community is not fully developed – in part due to microclimatic constraints in these vegetation stands of rather open structure (cf. Martius et al. 2004a). In these systems, consequently, litter should accumulate on the forest floor (high stocks), because the activity of soil organisms is reduced.

In the present paper we report on litter stocks and litter fall in the study sites and relate these to litter quality (carbon and nitrogen contents), to microclimatic conditions and to soil parameters. We then discuss the decomposition rates derived from litter fall and stock data and draw conclusions on the functionality of the biogenic decomposition process in these agroforestry systems.

## Material and methods

### Study sites

The study area belongs to the agroforestry research station Embrapa Amazônia Ocidental, which is located close to the city of Manaus, Amazonas, Brazil (3°8' S, 59°52' W). The region is flat without elevations (altitude 44–50 m a.s.l.; Corrêa, personal communication). The investigations took place in an area that was cleared from primary rainforest in 1979/1980, when a plantation of rubber trees (*Hevea brasiliensis*; Seringueira) was established. This plantation was abandoned in 1984, and then secondary growth started to establish. Finally, in 1992, the secondary growth was cut and burned. Since then, the area has been used for a cooperative agroforestry research program between the Embrapa-Amazônia Ocidental, Manaus (Brazil) and the Institute of Applied Botany, University of Hamburg (Germany) (Lieberei and Gasparotto 1998). The study was based on the experimental installation of different multi-crop systems that were thought to be economically viable in the region and, at the same time, ecologically sustainable (Feldmann et al. 1995; Lieberei et al. 1997).



Figure 1. Sample sites of the study: (a) primary rainforest (FLO); (b) secondary forest (SEC); (c) polyculture plantation site (POA, POC) showing a row of planted trees surrounded by upcoming secondary vegetation.

The experimental area was divided into five blocks and 90 experimental plots of  $32 \times 48$  m each. For the present study, two of these plots (POA in block A and POC in block C; the latter located close to the edge of the primary forest) were sampled. We also sampled two additional plots ( $40 \times 40$  m each), one in a secondary (SEC) and the other in a primary (FLO) forest (Figure 1). The primary forest in the region of central Amazonia near Manaus has been described in Gentry (1990) and Ribeiro et al. (1999). Both sites were within a distance of less than 200 m to the polyculture sites. For details see Beck et al. (1998a,b) and Höfer et al. (2000). Climate data (rainfall) were measured at Embrapa's climate station.

#### Vegetation

Approximately 1100 species of vascular plant species were found in the study plots (Preisinger et al. 1994, 1998), the most frequent of which are listed in Table 1. In the polyculture plots, originally four different

tree crop species of commercial use were planted in rows in 1992: rubber trees (*Hevea brasiliensis*), a low quality wood species (*Schizolobium amazonicum*, locally known as Paricá) and two native high quality wood species (*Swietenia macrophylla*, Mogno, and *Carapa guianensis*, Andiroba). Three rows of rubber and Paricá trees spaced 4 m were planted alternating with two rows of Mogno and Andiroba trees spaced 7 m; the distance between all rows was 10 m. During the time of the present study (1997–1999), the planted Andiroba trees were still thriving, but Paricá had already died at most sites. Between the planted rows, upcoming secondary vegetation was tolerated.

During the study period, it was dominated by *Vismia guianensis* (Guttiferae), a treelet whose population influenced especially the litter fall in these sites. The studied secondary forest area was growing since 1984 on a former abandoned rubber plantation; during the study period it was dominated by *Vismia guianensis*, *Miconia* and *Bellucia* spp. (Preisinger et al. 1998).

Table 1. Vegetation characteristics and site use histories of the study sites in Central Amazonia (Embrapa Amazônia Ocidental near Manaus, Brazil; data from Preisinger et al. 1998); *n*=number of species of vascular plants found in an area of 0.16 ha.

Vegetation type	Site history	<i>n</i>	Key families	Dominant species
Primary forest (FLO)	Extensively used for timber extraction	500	Sapotaceae Chrysobalanaceae Burseraceae Lecithidaceae	<i>Astrocaryum</i> sp. <i>Oenocarpus bacaba</i> <i>Eschweilera</i> spp.
Secondary forest (SEC; 8 years old)	Primary forest slashed and burned; rubber trees planted and abandoned 2 years later	200	Melastomataceae Moraceae Rubiaceae Bignoniaceae	<i>Vismia guianensis</i> <i>Miconia</i> spp. <i>Bellucia</i> spp.
Polyculture sites (POA, POC)	Slashed and burned twice; timber trees planted in rows	30–60	Guttiferae Meliaceae Caesalpiniaceae Meliaceae Euphorbiaceae	<i>Vismia</i> spp. <i>Carapa guianensis</i> (crop) <i>Schizolobium amazonicum</i> (crop) <i>Swietenia macrophylla</i> (crop) <i>Hevea brasiliensis</i> (crop)

Table 2. Soil properties of the four study sites (for site codes see Table 1).

	FLO	SEC	POA	POC
Vegetation	Primary forest	Secondary forest	Polyculture systems	
Soil type	Xanthic Ferralsol (sandy clay): 60% clay, 25% sand, 15% silt			
pH value (CaCl <sub>2</sub> )	4.0 ± 0.2	4.0 ± 0.1	4.2 ± 0.1	4.0 ± 0.2
WHC <sub>max</sub> (%)	864	797	768	n.d.
C content (%)	3.5–4.5	2.5–3.3	2.5–3.5	3.1–4.5
N content (%)	0.26–0.31	0.21–0.25	0.20–0.26	0.23–0.30

WHC<sub>max</sub> – maximum water-holding capacity.

### Soils

Soil properties were determined according to ISO guidelines (ISO 1992, 1994a,b; slightly adapted to the conditions of the EMBRAPA laboratory). The soil in the region is a Xanthic Ferralsol according to the FAO/UNESCO classification (FAO/UNESCO 1990), known in Brazil as 'latossolo amarelo' (Corrêa 1984). The main mineral is Kaolinite. The topsoil (0–10 cm) in the polyculture site is a sandy clay in the German classification (Müller 1995; Table 2). The clay content increases to 80% (14% sand and 6% silt) at a soil depth of 60–80 cm. The same tendency was found by Corrêa (1984) for a nearby primary forest site: 81–9–10% (clay–sand–silt) in 0–8 cm depth and 91–5–4% in 70–104 cm depth, and in spite of slightly differing values in Vohland and Schroth (1999) and Ulbrich (1999), differences in particle size distribution in the four sites seem to be negligible. The soil pH of the four sites also did not show large differences (Table 2). Soil pH values between 3.5 and 4.5 are given by

Müller (1995), Vohland and Schroth (1999), Ulbrich (1999), and Corrêa (1984). The carbon content in the top soil layer showed a range of 2.5–4.5% without clear differences between FLO and POC and between SEC and POA, but with significant differences between these two pairs (Table 2). For the primary forest, Corrêa (1984) and Ulbrich (1999) determined C values in the uppermost 8 (10) cm of 2.0 and 2.5% C, respectively. The results differ from those measured in the same area by Müller (1995) who, using other methods, found a much higher C variability in various polyculture plots (0.3–6.8% C) than in the secondary forest (2.4–5.3% C). The absolute N content differed only slightly between the four sites (FLO 0.8%, POC 0.7%, POA and SEC 0.6%). However, much lower values (0.2% N) were found by Corrêa (1984) and Ulbrich (1999) for primary forest. The only marked differences between the sites thus appear to be in soil moisture, as the water-holding capacity at FLO was higher than in the other sites (Table 2). Only small horizontal differences within the sites

were found in pH and actual moisture (Höfer et al. 2000).

#### *Litter sampling*

##### *Litter fall*

Falling litter was collected weekly by simple collectors with a basal area of 0.25 m<sup>2</sup> (50×50 cm). A collector consisted of a wooden frame 8 cm high and a nylon screen mesh suspended to a height of 50 cm above the ground. Twenty of such samplers were used in each of the forest areas (FLO, SEC), and 10 samplers in each of the two plantations (POA, POC). The collectors were distributed at random within the areas and their positions were maintained throughout the study. The collected litter was manually separated into fractions (leaves – fine wood < 1 cm diameter – coarse wood > 1 cm diameter – flowers and seeds – fine matter going through a 5-mm mesh sieve), then oven-dried at 65 °C for 4 days and weighed (dry weight). For the analysis, average weekly values were calculated and then multiplied with 52 to obtain the annual litter fall at each site. The study lasted from 27 July 1997 to 29 March 1999 (87 weeks). The average weekly litter fall was calculated on the basis of all weeks and all collectors, or 88×20=1760 data points for FLO and SEC, and 88×10=880 data points for POA and POC.

##### *Litter stocks*

Litter stocks were collected monthly with soil corers (21 cm diameter) at randomly chosen points in the study sites. Once every month between 26 August 1997 and 2 March 1999, 20 such samples were taken per site in FLO and SEC, and 10 samples per site in POA and POC. The corer was pressed into the soil and all litter inside the rim was manually collected into plastic bags. The dry weight was determined as for litter fall. The material from one sampling event every 3 months was manually separated into the same fractions as for litter fall plus roots for the analysis of the fraction distribution. However, as the percentage of roots in the material was very low, we decided not to correct the litter stocks for roots.

##### *Canopy closure*

Canopy closure was recorded with a digital camera (Sony DSCP5) in a standardized procedure (cf. Martius et al. (2004a) for details). Ten shots of the canopy were taken at random points in each site, with the

camera mounted on a tripod pointing vertically upwards. We then transformed the original color picture into a graph containing only black and white pixels using a standard commercial graphics software package (PaintshopPro 7). Canopy closure is the percentage of black pixels in the picture.

##### *Carbon and nitrogen analyses*

The carbon and nitrogen contents of the substrates were determined with a VARIO EL elemental analyzer (Elementar, Hanau). Details of the procedure are given in Höfer (2000). Litter fall samples were mixed samples for each site; for every month between August 1997 and March 1999 (19 months) one weekly sample was used for analysis. From the analysis of C and N in litter stocks, samples in three-weekly intervals (August and November 1997, and March, June, September, and December 1998) were selected; all samples from each site were mixed for analysis. Thus, a total number of 228 litter fall and 72 litter stock samples was analyzed for C and N.

##### *Data processing*

The study period of 87 weeks included two dry seasons but only one rainy season. Litter fall is related to climate seasonality (Martius 2004) and therefore, if total annual litter fall is to be calculated, a full year must be taken into account. In order to achieve that, two slightly overlapping annual data sets were produced referring to the periods of 1997–1998 and 1998–1999.

Due to technical reasons, litter fall was sampled in regular 1-week intervals, whereas stock sampling occurred at irregular intervals (2–5 weeks). For the correlation of litter fall and stocks and the determination of decomposition coefficients, the time intervals of litter fall and stock data had to be adjusted in order to relate both data sets to the same time periods. Assuming that the litter stocks are predominantly determined by the litter fall that is produced during the 4 weeks before the day of collection, we corrected the data set so that the litter fall data of the 4-week interval immediately before every stock sampling were related to that date. In a few cases where stock sampling was repeated after less than 4 weeks, this led to an overlap of the litter fall data from some weeks.

For the correlation between rainfall and decay rates, a 95% prediction interval was calculated using

Table 3. Annual litter fall (dry weight,  $\text{t ha}^{-1} \text{ year}^{-1}$ ) as means and standard deviations (S.D.) in each site, calculated for two full annual periods within the study period 1997–1999 (see text; for site codes see Table 1).

Area	1997–1998 <sup>a</sup>		1998–1999 <sup>b</sup>	
	Mean	S.D.	Mean	S.D.
FLO	9.50	8.81	7.93	6.59
SEC	7.19	7.76	7.57	7.64
POA	6.42	4.89	6.47	4.11
POC	7.19	6.19	8.72	6.03

<sup>a</sup>22 July 1997–21 July 1998; <sup>b</sup>30 March 1998–29 March 1999.

Sigmaplot 8.0. ANOVAs were calculated with Sigma-stat 2.03.

## Results

### Litter fall

The average weekly litter fall was highest in FLO ( $17.18 \pm 15.49 \text{ g m}^{-2}$ ), and decreased in the order  $\text{POC} > \text{SEC} > \text{POA}$  (Appendix 1). Annual litter fall was calculated for two overlapping periods of 1 year each (Table 3), and was always lowest in POA. In 1997–1998, litter fall was highest in FLO, but in 1998–1999, it was highest in POC. Average litter fall and standard deviation in FLO ( $9.50 \pm 8.81$  and  $7.93 \pm 6.59 \text{ t ha}^{-1} \text{ year}^{-1}$ , respectively, in 1997–1998 and 1998–1999) were in the range of litter fall recorded in other central Amazonian sites (e.g.,  $7.1 \pm 8.6 \text{ t ha}^{-1} \text{ year}^{-1}$  in nearby Reserva Ducke; cf. Martius (2004) for a regional comparison of litter fall data). The huge standard deviations indicate a high variability in litter fall between microsites (i.e., between the single collectors).

### Variability of litter fall

The relative variation of litter fall in SEC was higher than in the other sites (in five collectors, the standard deviation exceeded the average; Figure 3). The standard deviation in POA and POC never exceeded the average, pointing to the relatively high homogeneity of the vegetation structure in these stands. One large peak in SEC recorded on 21 December 1998 (Figure 3; week 9) was due to the highest single litter fall value recorded (85.1 g in one collector, against an average litter fall of 2.5 g per collector in all other collectors in this week). This outlier was due to a

large amount of coarse dead wood (98% of the material collected on this occasion was coarse dead wood).

### Fraction distribution

Leaves always represented the largest fraction in all sites, accounting for 67–82% of the litter fall. Fine wood was always the second largest fraction (14% in FLO and 8–11% at the other sites). Whereas coarse wood accounted for 2.8% of the litter in FLO, and 1.6% in SEC, almost none of it was produced in POA and POC (0.1% in each). The portion of flowers and seeds was comparably high in all sites, but fine matter in FLO (9%) was two times higher than fine matter in the other sites (3–5%) (Figure 2a), and this difference was statistically significant at  $P=0.05$  (Kruskal–Wallis ANOVA on ranks).

### Variability of different litter fall fractions

The production of the leaf fraction always has the lowest variability (Table 4); this is more expressed in the secondary forest and in the plantations, which are relatively simply structured because they are dominated by cohorts of trees of similar age. The coarse wood fraction is highly unpredictable (see above); principally in the plantations where dead wood rarely was produced.

### Seasonality

In all sites, the largest litter fall was observed in October 1997 (weeks 9–11 in Figure 3), at the end of a very dry period. Litter fall was lowest from February to March 1998 (weeks 28–35 in Figure 3), and increased again during the dry season of 1998 (August–September; weeks 50–65). In FLO, annual litter fall was higher in 1997–1998 than in 1998–1999, but in the other sites, annual litterfall was higher in 1998–1999 (Table 3). In FLO, monthly litter fall and monthly rainfall are inversely correlated ( $r^2=0.6$ ). This means that monthly litter fall in a rainforest stand can be predicted from rainfall (Table 5). The correlation is much weaker in the other sites. A similar correlation was found in a rainforest nearby (Martius 2004).

Litter fall and its variability were highest in the dry season of 1997 in all sites (Figure 3: weeks 0–12). In contrast, in the preceding years (1993–1996) no significant inter-annual variation of litter fall in the dry season was detected in a nearby rainforest (Martius 2004). This may point to an effect of the 1997 El Niño event (Wolter and Timlin 1998) on litter fall.

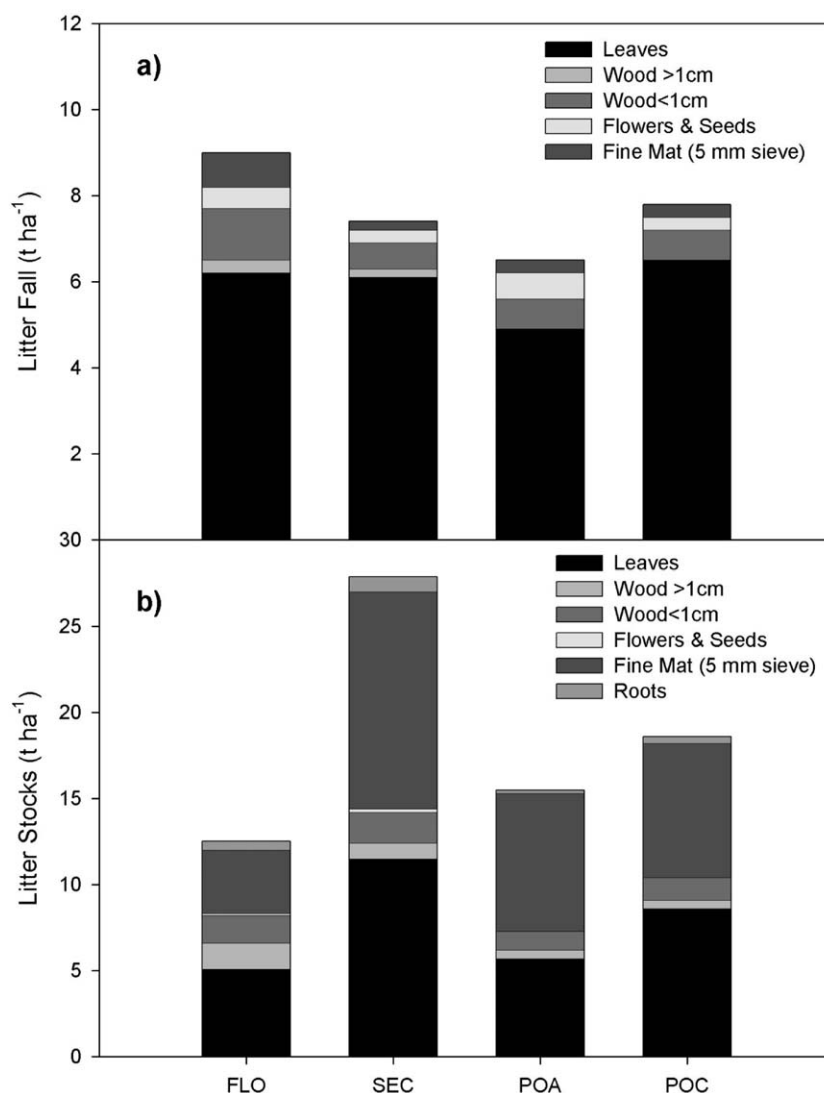


Figure 2. (a) Distribution of litter fall into fractions: average of 10 (FLO, SEC) and 5 (POA, POC) collectors and 88 weeks. For standard deviation as % of average cf. Table 6. (b) Distribution of litter stocks into fractions: average of 20 (FLO, SEC) and 10 (POA, POC) collections in 3-monthly intervals. Note that roots is included as an additional fraction here.

### Carbon and nitrogen in litter fall

#### Within-site variability

First, we analyzed the variance of C and N contents in the litter within the areas by determining the C and N concentration of the litter of every single collector separately, based on the litter fall material collected in the week before 11 August 1997 (Table 6). The nitrogen concentration of the fallen litter in single collectors (all sites) ranged from 0.8 to 2.4%. The carbon concentration ranged from 45.1 to 52.8%, and the C/N ratio in litter fall ranged from 57.6 to 18.7. Given

the much higher stand diversity in FLO than in the anthropogenic sites, it was surprising to see that the C/N ratios vary less between different samples in FLO than in the other sites (Figure 4).

#### Site differences

When comparing the monthly data sets (samples from all collectors of each area pooled), the highest average N concentration was found in FLO (1.4%) where consequently the C/N ratio was lowest (35.1; Table 7). The lowest average nitrogen concentration was

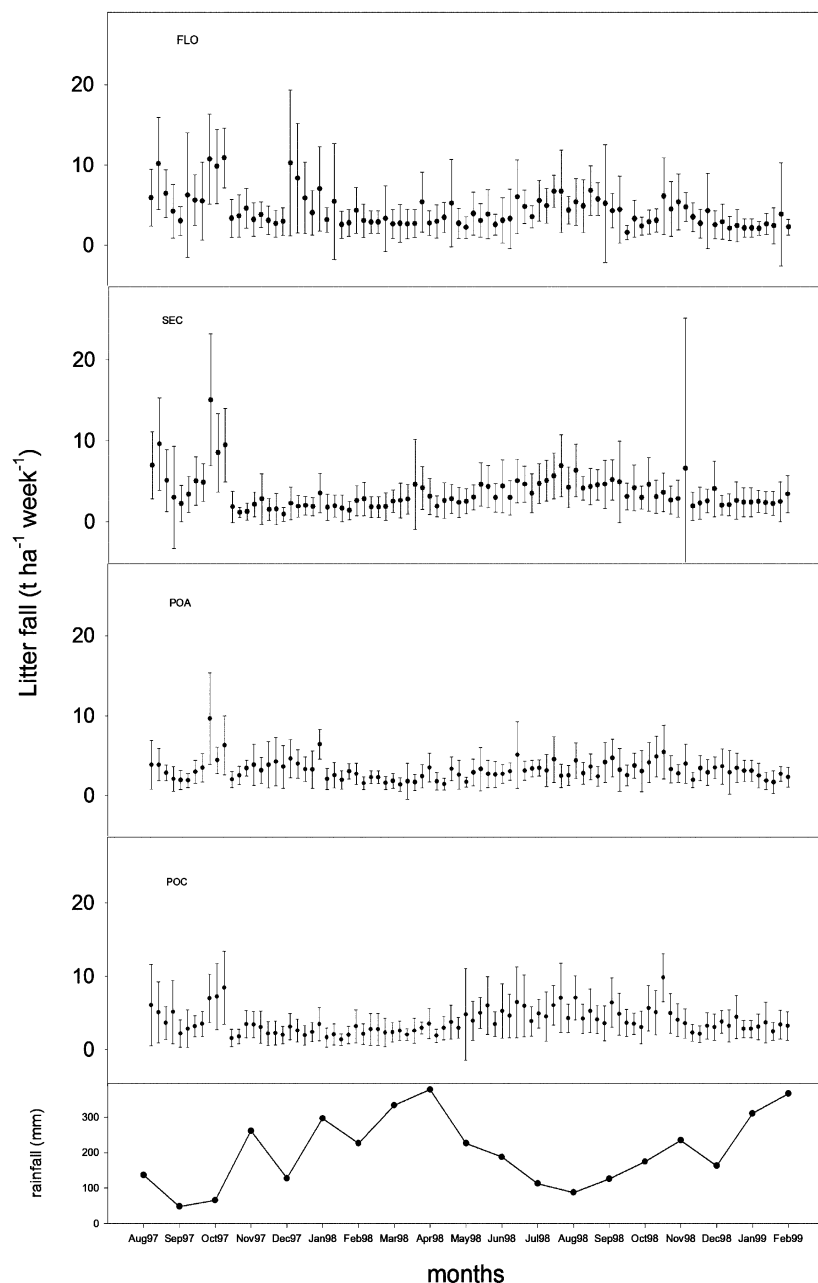


Figure 3. Mean weekly litter fall ( $\text{t ha}^{-1} \text{ week}^{-1}$ ), standard deviation for 20 (FLO, SEC) or 10 (POA, POC) litter samplers in the study area and monthly rainfall (mm).

found in litter fall samples from POC (1.3% N), and here the C/N ratio was highest (40.6).

The differences in N concentrations between FLO and SEC, and FLO and POA were significant. Also, the differences in C concentrations and C/N ratios between FLO and SEC, and between SEC and POC

were statistically significant (one-way ANOVA, Tukey test for pairwise comparison; Table 7). Average absolute N content of the litter fall (N concentration  $\times$  litter fall weight) over 20 weekly samples (August 1997 to March 1999) was highest in FLO, intermediate in POC and POA, and lowest in

Table 4. Variability of fractions in litter fall (cf. Figure 3): standard deviation as % of mean. Mean of 10 (FLO, SEC) and 5 (POA, POC) collectors and 88 weeks (for site codes see Table 1).

Area	Leaves	Wood > 1 cm	Wood < 1 cm	Flowers and seeds	Fine matter (5-mm sieve)
FLO	22.4	239.7	75.5	109.7	72.2
SEC	15.8	475.5	88.8	113.6	75.4
POA	15.3	938.1	71.3	114.4	59.9
POC	11.6	685.4	74.3	96.7	69.4

Table 5. Linear regressions ( $y=ax+b$ ) of monthly litter fall ( $\text{t ha}^{-1} \text{ month}^{-1}$ ) and monthly rainfall (mm) for the study sites primary forest (FLO), secondary forest (SEC), and the plantation sites (POA and POC) (data set August 1997–February 1999; for site codes see Table 1).

Area	<i>a</i>	<i>b</i>	$r^2$
FLO	-0.0017	1.006	0.582
SEC	-0.0014	0.844	0.299
POA	-0.0006	0.640	0.224
POC	-0.0009	0.775	0.176

SEC (Table 8). The differences were statistically significant (Kruskal–Wallis ANOVA,  $P=0.011$ ) and multiple comparison (Tukey) showed that POA and SEC differed significantly from FLO ( $P < 0.05$ ). Using the absolute N content from these mixed samples from each area, we calculated an average accumulated input of  $9.1 \text{ g N year}^{-1} \text{ m}^{-2}$  in POA,  $11.2$  in POC,  $10.3$  in SEC and  $14.4 \text{ g N year}^{-1} \text{ m}^{-2}$  in FLO (Figure 5).

#### Litter stocks

The litter stocks on the forest floor in SEC were by far the largest (Table 9). The monthly averages (over all stock samples per site) in SEC differed significantly from the stocks in all other sites (one-way ANOVA, Tukey test for pairwise comparison,  $P=0.001$ ). The litter stocks in FLO, POA and POC did not differ significantly from each other. These findings are valid for the whole study period (averages from 87 weeks) and also for the data sets from the two single annual periods (Table 10). Within the sites, no significant differences of average litter stocks between the single annual periods were found.

Stocks of large (coarse) dead wood in the study sites have been assessed on one occasion (the volume was assessed and converted to biomass; Martius et al. 2004b). They follow the sequence FLO ( $24.5 \text{ t ha}^{-1}$ ) > POC ( $12.1 \text{ t ha}^{-1}$ ) > SEC ( $4.0 \text{ t ha}^{-1}$ ) > POA ( $2.4 \text{ t ha}^{-1}$ ). Thus, whereas leaf litter

stocks are highest in SEC, large wood litter stocks are highest in FLO, and a very small amount of large wood litter is found in the plantations. Wood biomass is roughly double that of small leaf litter biomass in FLO, but corresponds to only about 15–75% of leaf litter stocks in the plantations.

The inverse linear regression of monthly litter stocks in the four sites and monthly rainfall (as climate indicator) is only weakly correlated (Table 11); however, the power of the performed tests (with  $\alpha=0.05$ ) generally is too low to exclude the existence of a correlation. Data sets covering a longer period would be needed to confirm this regression.

#### Fractions

In the litter stocks, leaves and fine matter were the two largest fractions. Leaves accounted for 37–46%, and fine material for 30–52% (Figure 2b). Fine and coarse wood together accounted for 25% of the litter stocks in FLO, but only for about 10% in all other sites. Thus, leaf litter had a much lower percentage in litter stocks than in the litter fall. This reflects the fact that litter on the forest floor is much more degraded than freshly fallen litter. The percentage of flowers and seeds was negligible in all sites. The percentage of roots in the litter stocks was 4% in FLO and 1–3% in the other sites. It was not possible to distinguish between live and dead roots in the collected material (although probably dead roots accounted for the larger part of the material).

#### Carbon and nitrogen in litter stocks

The samples from the primary forest site showed slightly higher N concentrations (1.36%) than the samples from the other sites, with SEC at the lower end (1.29%). The average C concentrations were rather similar for all areas except POA, where they were lower. The C/N ratios were similar in all areas (Table 12). The differences between areas in N concentrations were not significant (Figure 6a), but the absolute N contents of the stocks of the different ar-

Table 6. Nitrogen and carbon concentrations and C/N ratios as means and standard deviations (S.D.) in all samples of one data set (within-site variability – August 1997) of litter fall (differences are not significant).

	N (%) mean	S.D.	C (%) mean	S.D.	C/N mean	S.D.
Whole data range	1.35	0.29	49.2	2.65	38.0	7.26
FLO	1.42	0.27	48.4	1.67	35.1	5.85
SEC	1.32	0.21	50.4	1.69	39.2	5.97
POA	1.35	0.26	50.5	0.71	38.8	8.31
POC	1.25	0.45	47.0	4.65	40.6	9.95

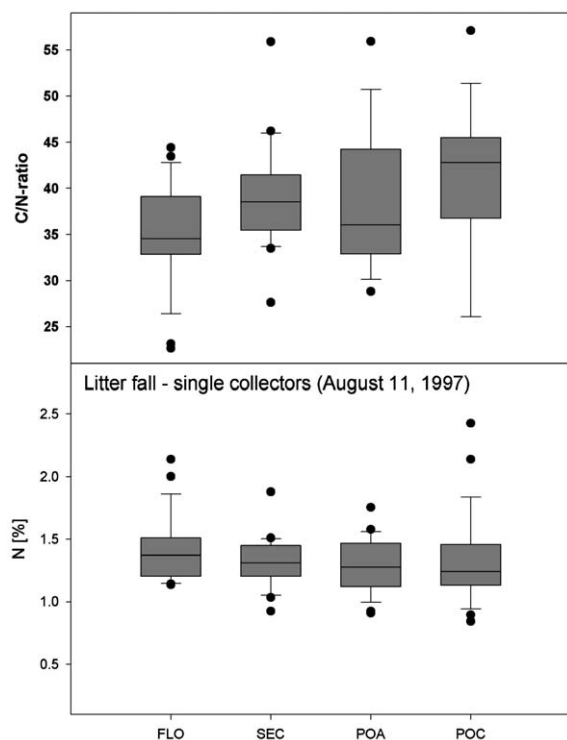


Figure 4. Box plots of C/N ratio and nitrogen concentration in single collectors from one sampling date (11 August 1997) in the four study sites. Line in box – median; dotted line – mean; upper/lower box margins – 75th/25th percentiles; whiskers – 90th/10th percentiles; points beyond whiskers – outliers.

was significantly different (Figure 6b; SEC versus all other areas,  $P < 0.001$ ), due to the accumulation of litter in the secondary forest.

#### Canopy closure

Canopy closure was 87–88% in POC and FLO, and 80–81% in SEC and POA (Table 13). It was therefore well linearly correlated with litter fall ( $r^2=0.798$ ;  $P=0.107$ ), but not with litter stocks ( $r^2=0.3596$ ;  $P=0.401$ ). Whereas litter fall depends mainly on the

amount of leaf material present in the canopy which is captured by canopy closure, litter stocks are a product of litter fall and decomposition rate (see below) and are therefore not related to canopy closure.

## Discussion

### Litter fall

Litter fall differed between the study areas of natural rainforest, secondary forest and agroforestry sites (Table 3). These differences are not likely to be related to soil parameters, because these did not differ much between the sites (Table 2). However, litter fall was linearly correlated to canopy closure, which reflects the stand structure. The plant species diversity in the primary forest site – representing the dominant and very diverse natural ecosystem in the region – was two times higher than in the secondary forest stand, and 10 times higher than in the plantation sites (Table 1). This goes along with a much more complex stand structure in FLO, with high trees and several storeys of vegetation and a much higher stand biomass. On the other hand, microclimate extremes, e.g., in soil temperature and air humidity, are most pronounced in POA (Martius et al. 2004a), and drought is known to induce litter fall (Martius et al. 2004a,b). All this is consistent with a high litter fall in FLO.

The difference in canopy closure between the two polyculture systems POC and POA also explains the higher litter fall in POC. Some differences between the single plantation sites in the different blocks of the experimental area are not related to the treatment but stem from the land use history prior to the experiment. For example, the total number of plant species in experimental block A (to which POA belongs) was lower than that in block C (where POC is situated; Preisinger et al. 1994). Also, POA is much

Table 7. Nitrogen and carbon concentrations and C/N ratios of litter fall samples as means plus standard deviations (S.D.) over all weeks.

	N		C		C/N	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
FLO	1.43 a	0.13	48.90 b	0.79	34.56 b	3.46
SEC	1.27 b	0.10	50.47 a	1.08	39.84 a	2.65
POA	1.30 b	0.13	49.29 b	0.54	38.19 a	4.13
POC	1.35 ab	0.11	48.88 b	0.93	36.50 ab	3.36

Numbers followed by the same letter in a column are not significantly different at  $P < 0.05$  (Tukey test) (for site codes see Table 1).

Table 8. Absolute nitrogen contents in litter fall (one mixed sample of one week from every month was analysed) and accumulated N-inputs (for site codes see Table 1).

	Relative N concentration (%)				Litter weight (g collector <sup>-1</sup> week <sup>-1</sup> )				N content of litter fall (g m <sup>-5</sup> week <sup>-1</sup> )			
	FLO	SEC	POA	POC	FLO	SEC	POA	POC	FLO	SEC	POA	POC
Means	1.42	1.28	1.31	1.34	4.83	3.80	3.36	4.03	0.28	0.20	0.17	0.22
N (g per 20 weeks and m <sup>2</sup> )									5.52	3.96	3.50	4.31
N (g year <sup>-1</sup> m <sup>-2</sup> )									14.4	10.3	9.1	11.2
N (kg year <sup>-1</sup> ha <sup>-1</sup> )									143.5	103.0	90.9	112.1

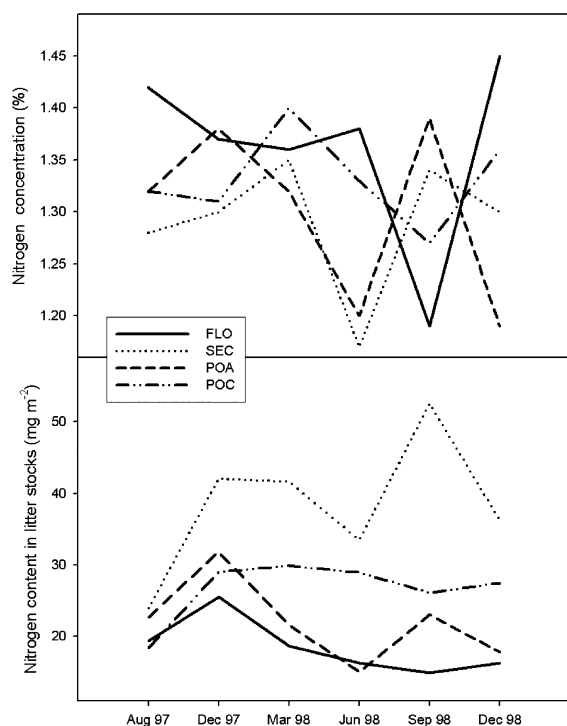


Figure 5. Nitrogen concentration (%) and nitrogen content (mg m<sup>-2</sup>) in litter stocks in the four study sites.

more exposed to sunlight than POC, which in the afternoon is shaded by an adjacent block of primary forest. Although the study of intercropping was not

Table 9. Mean monthly litter stocks in the study sites during the study period ( $n=20$  months; August 1997–March 1999), and average stocks based on 1-year periods (for site codes see Table 1).

Area	Average stocks (t ha <sup>-1</sup> ) ± S.D.	S.D. as % of average
FLO	11.98 ± 4.27	36
SEC	24.70 ± 3.43	14
POA	15.06 ± 3.03	20
POC	16.19 ± 4.12	26

Table 10. Mean litter stocks (dry weight, t ha<sup>-1</sup> year<sup>-1</sup>) in each site, calculated for annual periods within the study period 1997–1999 (see text; for site codes see Table 1).

Area	1997–1998 <sup>a</sup>		1998–1999 <sup>b</sup>	
	Mean	S.D.	Mean	S.D.
FLO	12.68	4.46	10.90	1.42
SEC	22.82	8.71	26.64	5.98
POA	14.75	7.12	14.23	5.10
POC	16.02	8.21	15.26	4.79

<sup>a</sup>22 July 1997–21 July 1998; <sup>b</sup>30 March 1998–28 March 1999.

an objective of this study, this result points to the importance of interspersing agroforestry systems with natural vegetation in Amazonia, to capture ecological benefits offered by a neighboring rainforest.

Table 11. Linear regressions ( $y=ax+b$ ) of monthly litter stocks ( $t\ ha^{-1}$ ) and monthly rainfall (mm) for the study sites primary forest (FLO), secondary forest (SEC), and the plantation sites (POA and POC) (full data set; August 1997 to February 1999).

Area	<i>a</i>	<i>b</i>	<i>r</i> <sup>2</sup>
FLO	-0.0193	15.98	0.278
SEC	-0.0250	29.90	0.095
POA	-0.0296	21.21	0.238
POC	-0.0265	21.68	0.161

#### Consequences for soil organisms

Soil fauna depending on leaf litter as its main food resource can expect a much higher litter quantity in the primary forest than in the other sites. Also, the difference in plant species composition (Table 1) means that a high variety of different litter types is offered. The diversity of the litter fall is particularly low in SEC and the plantations, sites that were dominated by a few tree species only (*Vismia guianensis*, *Miconia* sp. and *Bellucia* sp.) during the time of this study (Table 1), a possible constraint for some soil fauna taxa.

The litter fall in the primary forest was strongly correlated to rainfall, as in a previous study (Martius 2004). The rainforest plant seasonality is linked to rainfall seasonality. This correlation was not observed in the plantation sites. This is probably due to the fact that the latter are dominated by only a few tree species that have a different litter fall seasonality than most rainforest trees. This could represent a further constraint for some soil fauna groups (for example, in termites life cycles are adapted to the seasonality of rain and litter fall, cf. Martius 2001).

On the other hand, inter-annual differences in litter fall are rather small in all sites (Table 3). For primary forest, this is consistent with previous findings (Martius 2004), but the result is astonishing in view of the large climatic differences between the year 1997 and the other years (Martius et al. 2004a). The often large variation of population size of litter-inhabiting arthropods between the seasons and years (Hanagarth et al. 2004) cannot be explained by inter-annual litter fall differences.

#### Litter stocks

Not only were the average litter stocks in FLO much lower than in the other sites (Table 9), but also in almost all months of the study period the lowest litter stocks were found in the primary forest (Figure 6). No

correlation between litter stocks and canopy closure was found, because litter stocks are a product of litter fall and decomposition rate.

#### Carbon and nitrogen

The nitrogen content of leaves is often used as an indicator of litter quality (Swift et al. 1979), and the C/N ratio is used as indicator of decomposability. The C/N ratios in both litter fall and stocks in FLO and POC were significantly lower than in the other two sites (Tables 7 and 12). This indicates a higher overall decomposability of the litter in these two sites, although the higher standard deviations also show that the litter is of much more inhomogeneous quality than in SEC and POA.

The litter fall collected in the primary forest (FLO) contained slightly but significantly more nitrogen than the samples from all three anthropogenic sites (SEC, POA and POC). These differences could at first sight be attributed to species-specific nitrogen contents of the leaves of trees from the different plant associations present in the sites. However, the dominating litter producers in the anthropogenic sites are *Vismia* trees, and their leaves did not show distinctly lower nitrogen contents or higher C/N ratios when compared with, for example, the primary forest tree species Andiroba or Mogno (*Carapa guianensis* and *Swietenia macrophylla*, respectively; Höfer 2000). The higher nitrogen contents of the litter fall in FLO could well reflect a better nutrient supply of the trees over many years. This becomes clear when we look at the build-up of nitrogen through time, because the relatively small initial differences in N content in weekly litter fall samples sum up to considerably large differences in nitrogen input over long periods. Similar differences are found in the litter stocks, where nitrogen concentrations are always highest in FLO. However, higher total N stocks are found in SEC because the lower N concentration is compensated for by the high litter accumulation here.

#### The decay coefficient

The decay coefficient is an indicator of functioning decomposer communities. It is generally calculated on the basis of annual data of litter stocks (S) and litter fall or production (P). Here, we used monthly litter fall and stock values to calculate the decomposition rate on a monthly basis. This allowed observation of the decay processes at a very fine time resolution

Table 12. Mean C and N contents and C/N ratios in the litter stocks of the four study sites (for site codes see Table 1).

Site	N concentration (%)		C concentration (%)		C/N ratio	
	Mean	S.D. (%)	Mean	S.D. (%)	Mean	S.D. (%)
POA	1.30	6.85	40.43	13.52	31.01	10.29
POC	1.33	3.36	42.81	6.06	32.11	7.33
SEC	1.29	4.96	42.14	9.05	32.69	8.86
FLO	1.36	6.76	42.53	7.49	31.44	13.15

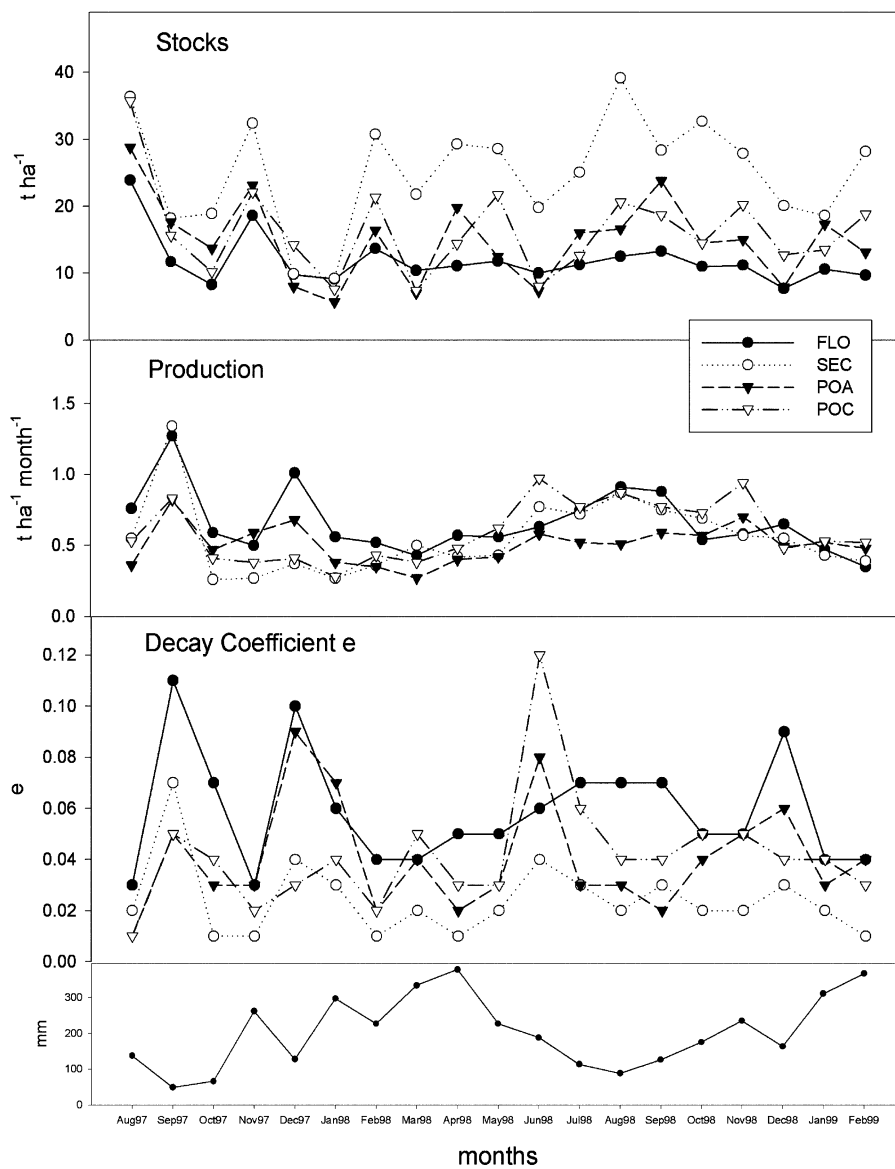


Figure 6. Monthly litter stocks ( $S$ ;  $\text{t ha}^{-1}$ ), litter production ( $P$ ;  $\text{t ha}^{-1} \text{ month}^{-1}$ ), decay coefficient ( $k_e = P/L$ ; no units), and rainfall (mm) for the study sites FLO, SEC, POA and POC.

Table 13. Canopy closure (%) as mean and S.D. in the study sites.

	Mean	S.D.
Primary forest (FLO)	88.0	3.9
Secondary forest (SEC)	80.5	7.3
Plantation site POA	79.9	14.4
Plantation site POC	87.0	3.5

(Figure 6). For example, the largest decay coefficients were observed in FLO in September and December 1997, and in POA in December 1997. This shows that the large litter stocks accumulated during the dry season of 1997 were rapidly decomposed in the following months in FLO and POA. Moreover, the decay coefficient in FLO was again high in December 1998. In other words, fast litter decomposition was observed in FLO in December both in 1997 and 1998, which may point to the effect of the heavy rainfalls prevalent in this month on litter decomposition (fast leaching and high humidity).

In an accompanying study (Höfer et al. 2004), the decomposition rate of *Vismia* leaves enclosed in litterbags was studied in the same sites in two series, one starting in the dry, the other in the rainy season. The decomposition rate calculated from these experiments was always higher in FLO than in the other sites, and the overall rates were higher than in the present study.

However, whereas only one litter type could be used in the litterbag study, and the results are rather punctual, the decomposition rate calculated from litter fall and stocks represents an integration over the decomposition processes involving all kind of litter available at the sites and over a much larger area. Therefore, the decomposition rates presented here represent much more the site-specific conditions than can be deduced from the litterbag experiments.

We calculated a linear regression between rainfall data and decay coefficients for all four plots. Due to the high variation in litter decay, these correlations have rather low  $r^2$  values; however, the 95% prediction interval shows that in FLO the monthly litter decay rate can be predicted – within very wide margins – from monthly rainfall (Figure 7). This is somehow contradictory to our findings reported above of larger litter fall during the dry season of 1997. It shows that several effects overlap – probably one is a general trend represented by the negative correlation of litter fall and rainfall, and another is accidental stress effects of prolonged or extreme droughts.

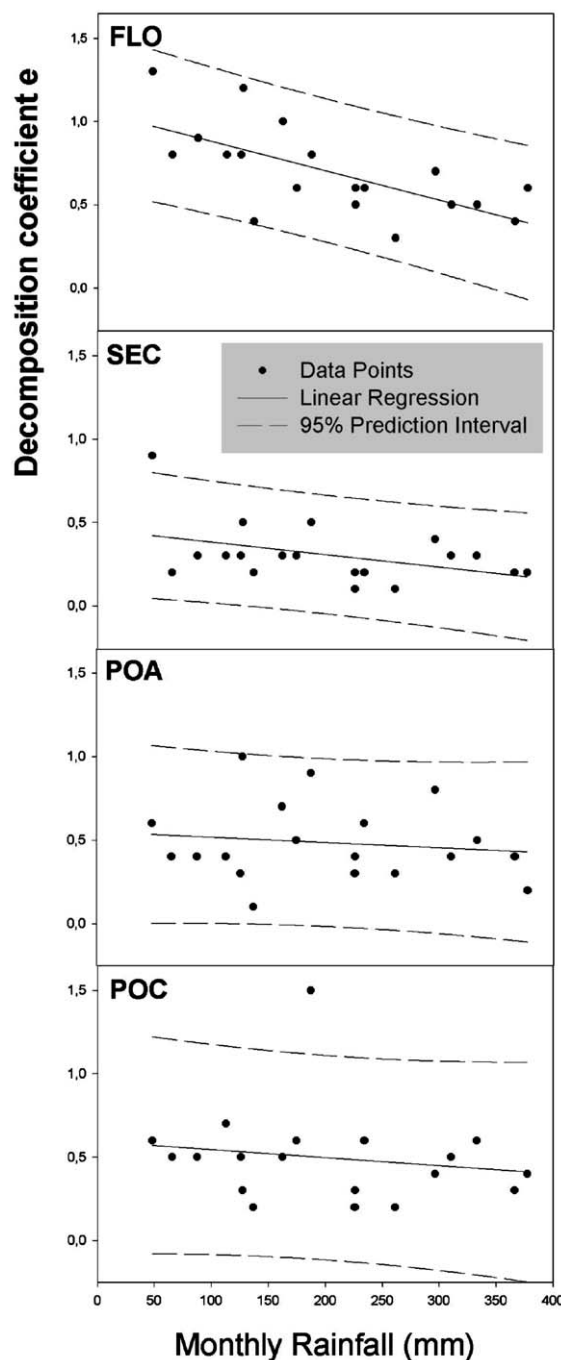


Figure 7. Regression between monthly rainfall and monthly decay coefficients (solid lines), and 95% prediction intervals (dashed lines) for each site.

The average monthly decomposition rate was highest for FLO (0.059), lower for POC (0.042) and POA (0.040), and lowest for SEC (0.024). In other

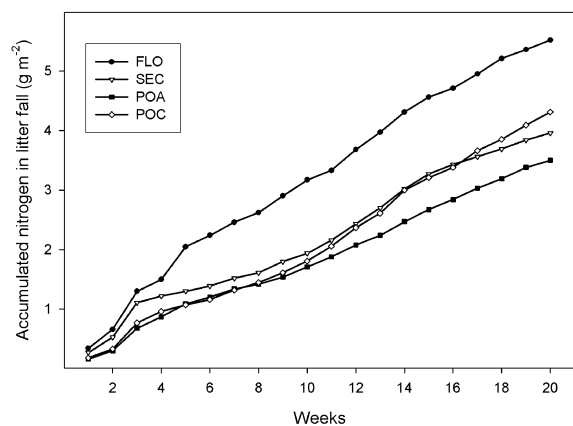


Figure 8. Accumulated nitrogen content in litter stocks in the different study sites in 20 weeks.

words, in the secondary forest site, which showed the largest litter accumulations in spite of a relatively low litter fall, the decomposition processes were very slow. In contrast, in FLO, which had a high litter fall but low stocks, the decomposition rates were high. The decay coefficients of the polyculture systems were in between, which means that here the decomposer communities seemed to perform better than in the nonmanaged secondary growth site. Like for nitrogen and C/N ratio, the decomposition rate also pits FLO and POC as the 'better' sites against SEC and POA.

The significantly higher decomposition rates in the primary forest and the higher transfer rates of nitrogen from leaves to soil could explain the higher nitrogen contents in the upper 5 cm of the soil in FLO. This hints at the existence of an optimized nutrient cycling in the primary rainforest that results in higher availability of nutrients for the plants, confirming the interactions proposed by Wardle (1999) between soil decomposer communities and plant growth.

Although the decomposer organisms are most active in natural rainforest sites, from the decomposi-

tion coefficients it seems that the agroforestry systems are also inhabited by soil organismic communities that are potentially functional with respect to the task of litter decomposition – at a lower rate than in FLO but higher than in SEC. Therefore, these systems seem to fulfill one requirement of low-input agroforestry systems, namely that of providing adequate conditions for soil organisms to provide beneficial ecological functions like the decomposition of organic debris and a subsequent recycling of nutrients. Although diversity and density of some soil macrofauna groups in the plantation sites are rather reduced (Römbke et al. 1999; Martius et al. 2004b), the decomposition rates confirm that the macrofauna community in these sites is still sufficiently large and diverse to maintain the decomposition processes at a functional level (Höfer et al. 2001). We conclude that from a soil-ecological viewpoint polyculture systems like those studied here have a beneficial effect on low-input agroforestry in Amazonia.

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This study (part of Project SHIFT ENV 52 'Soil fauna and litter decomposition') was funded by the German Ministry for Education and Research (Bundesministerium für Bildung und Forschung – BMBF), under number 0339675. We also thank the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for additional financial support. The research institution Embrapa-Amazônia Ocidental, Manaus, Brazil, logistically supported the study. Thanks are due to Francisco Aragão and Martina Meyer, who collected the litter during the study, and particularly to Gessiene do Nascimento Pereira and Valdinez Montoia, who processed the litter material in the laboratory and managed the data spreadsheets.

### Appendix 1

Average weekly litter fall (dry weight, g m<sup>-2</sup>) in the collectors of each site and calculated annual litter fall for 1998.

Area	Collector	Collector		Area	
		Average	S.D.	Average	S.D.
FLO	Q31	17.79	13.38	17.18	15.49
	AI 16	17.51	13.91		
	AF 08	14.92	12.18		

## Appendix 1. Continued.

Area	Collector	Collector		Area	
		Average	S.D.	Average	S.D.
	F 34	11.42	10.09		
	AM 18	14.70	12.33		
	AK 20	16.80	12.15		
	Q 16	21.92	19.77		
	AJ 29A	15.36	9.00		
	M 33	13.46	8.50		
	P 10	25.76	21.08		
	H 25	15.38	16.73		
	H 15	12.24	8.74		
	B 31	18.61	21.31		
	X 18	16.87	19.30		
	N 05	18.36	13.64		
	AD 13	16.62	14.88		
	AD 01	11.52	9.09		
	AE 22	20.99	18.41		
	T 09	17.30	12.82		
	AI 38	26.70	20.87		
SEC	Q 31	17.41	14.04	14.22	15.43
	AI 16	18.54	14.09		
	AF 08	15.36	39.35		
	F 34	14.89	11.13		
	AM 17	12.62	9.00		
	AK 20	12.68	10.04		
	Q 16	16.16	12.45		
	AJ 29	17.51	13.83		
	AM 33	12.69	9.52		
	P 10	22.42	23.12		
	H 25	11.61	10.75		
	H 15	9.62	7.25		
	B 31	11.34	11.35		
	X 18	15.65	13.57		
	Q 06	13.89	11.95		
	AD 13	14.65	11.30		
	AD 01	7.84	7.12		
	AE 22	15.89	14.60		
	T 09	13.22	15.48		
	AI 38	10.59	10.94		
POA	R 19	11.52	8.10	12.65	8.84
	J 07	13.47	8.98		
	M 25	18.37	11.98		
	W 26	14.55	8.44		
	F 11	11.22	6.76		
	G 02	8.47	6.61		
	S 23	13.69	9.33		
	C 05	11.09	7.62		
	AA 15	11.87	6.49		
	B 07	12.13	8.38		
POC	R 14	15.78	9.32	15.10	11.65
	AC 21	16.11	14.54		
	K 05	15.55	14.17		
	N 15	12.97	7.15		
	U 28	14.98	14.53		
	V 32	17.57	12.88		
	F 28	14.30	8.26		
	G 18	6.08	4.48		
	S 12	15.90	9.45		
	C 30	21.71	11.20		

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