

Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems

Hubert Höfer^{a*}, Werner Hanagarth^a, Marcos Garcia^b, Christopher Martius^c,
Elizabeth Franklin^d, Jörg Römbke^e, Ludwig Beck^a

^a Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, 76133 Karlsruhe, Germany

^b Embrapa-Amazônia Ocidental, rodovia AM-010 km 28, 69.011-970 Manaus, AM, Brazil

^c Center for Development Research (ZEF), Walter-Flex-Str. 3, 53113 Bonn, Germany

^d Instituto Nacional de Pesquisas da Amazônia (INPA), CP 478, 69.011-970 Manaus, AM, Brazil

^e ECT Ökotoxikologie GmbH, Böttgerstr. 2-14, 65439 Flörsheim, Germany

Received 18 August 2000; accepted 14 April 2001

Abstract – The soil biological conditions of two 5-year-old polyculture tree plantations in Amazonia were studied comparatively to a 13-year-old secondary forest and a nearby undisturbed primary forest. The polycultures had been planted to regenerate the soil degraded by land preparation and a former rubber tree monoculture. Abundance and biomass of functional groups of soil meso- and macrofauna were measured at three-months-intervals over 2 years and litterbag experiments with fauna exclusion were carried out. This paper concentrates on the description of the structure of the soil fauna communities, forming the background for an evaluation of the decomposition processes in polyculture plantations. Decomposition rates were strongly determined by the macrofauna particularly in primary forest, where large earthworms, termites and ants dominated the soil fauna. In the plantations, where litter originated predominantly from the non-planted, adventitious vegetation, an abundant decomposer fauna was found, in which however other groups or species dominated. Although decomposition rates in the plantations were about 60 % lower and soil biological variables like organic matter-, nitrogen-content and water holding capacity were slightly lower than in the primary forest, conditions seem favourable for a manipulation of the soil fauna by management of secondary vegetation and litter quantities.
© 2001 Éditions scientifiques et économiques Elsevier SAS

Soil fauna / decomposition / Amazonia / polyculture plantation

1. INTRODUCTION

In Amazonia large scale plantations of exotic tree species (e.g. *Eucalyptus urograndis* and *Pinus caribaea* in Jarí aiming to supply the pulp and paper industry [6]) and monocultures (e.g. *Hevea* in Fordlândia established in the forties to supply the international rubber demand) have replaced natural forest and resulted in highly degraded areas. Today, such attempts are considered as disastrous experiences [5]. Small scale degradation by “slash and burn” practice

of smallholders also sums up to considerable land consume. Nowadays the importance of “capoeiras” (local term for secondary forests) for vegetation and soil recovery and especially its improved management is widely recognized and led to several projects in Eastern Amazonia [4, 25, 27]. The necessity to slow deforestation leads to the needs to develop agroforestry systems on already deforested or secondary forest land. In an estimation of the Brazilian Agricultural Research Corporation, Embrapa [20] 5 million hectares in Brazilian Amazonia are indicated as already degraded pasture and an additional 5 million hectares of still productive pasture will enter in the first category within a decade. The total deforested area estimated at the end of the eighties was 43 million hectares [22].

*Correspondence and reprints: fax: +49 721 175 2884.
E-mail address: hhoefersmnk@compuserve.com (H. Höfer).

Recuperation of degraded land for sustainable use in the future is the focus of several projects in the German-Brazilian SHIFT Program (Studies of Human Impact on Forests and Floodplains in the Tropics). With the aim to develop economically and ecologically viable polyculture systems of fruit trees and timber wood producing species, German and Brazilian scientists set up a large experimental area on the site of the Brazilian Research Centre for Agroforestry in Western Amazonia [16]. A central idea was to enrich the plantations by controlled growth of secondary vegetation after the initial slash and burn treatment.

The importance of the soil fauna lies in their role as soil engineers and as a driving force in nutrient cycling by fragmenting and ingesting litter material and interacting with the microorganisms that decompose and mineralize the detritus. The reduction of soil fauna will decrease quality of carbon stocks in soils (Amelung et al., Submitted to Soil Biol. Biochem.) and, finally, will result in physical and chemical degradation of soil [14, 15, 24]. Soil organisms thus provide valuable ecosystem services that sustain soil quality and plant growth.

The aim of our study was to judge the soil biological conditions in the plantations with regard to the aspired sustainability of agricultural and forestry systems. We studied the structure of the soil fauna (i.e. presence and abundance/biomass of functional soil fauna groups) in correlation to the abiotic preconditions of the sites. Additionally variables, depending on the faunal activities, like decomposition rate were considered.

2. MATERIALS AND METHODS

2.1. Site description

The studied sites are situated in central Amazonia, about 30 km outside Manaus, within the experimental areas of the Brazilian research institute Embrapa-Amazonia Ocidental (02°53'S, 59°59'W). The region is dominated by dense primary lowland rainforest (terra firme) [12] on nutrient-poor soils classified as yellow clayey latosol (FAO: xanthic Ferralsol). Average annual rainfall is 2107 mm [11] and climate is characterized by a short dry season (monthly precipitation below 100 mm) from July to September and average monthly temperatures between 25 and 27°C.

The investigations took place in an area of rubber tree plantations that had been affected by the fungus *Microcyclus ulei*, were cut and burned in 1984 and then abandoned. In 1992 the secondary vegetation that had established was newly cut and burned to set up an experimental area divided into 90 plots of 32 × 48 m each [4]. Two of these plots (called POA and POC) of a polyculture system with 4 tree species planted (rubber tree - *Hevea* spp., one low quality wood species - *Schizolobium amazonicum* and two native high quality wood species - *Swietenia macrophylla* and *Carapa guianensis*) were studied from July 1997 to March 1999. In these plots spontaneous secondary vegetation (mainly *Vismia* spp.) was admitted between

the rows of trees. One plot of the secondary forest left over in 1992 as control area (called SEC) and one plot of primary forest (called FLO) in the close vicinity of the experimental sites were studied during the same period. For an extensive description of the sites and study design see [3].

2.2. Soil fauna

Soil fauna density and biomass in the four plots were assessed repeatedly (every 3 months, 8 times) collecting soil and litter samples with different methods. At every sampling event randomized soil samples were taken from every polyculture plantation ($n = 10$) and from every forest area ($n = 20$). Mesofauna was collected with soil cores of 6 cm diameter. Samples were separated in litter layer and top 5 cm soil layer and extracted in a modified Kempson apparatus. Enchytraeids were wet-extracted from additional samples ($n = 10$ or 20) taken with the same borer type from the same square metre. Further soil samples were taken for measurements of microbial respiration with an Infrared-Gas-Analyser. Macrofauna was sampled with soil cores of 21 cm diameter, which were treated in the same way and extracted in a Berlese-type extractor. Earthworms were extracted from soil by repeatedly pouring a 0.5 % formol solution to areas of 4 m² ($n = 1$ or 2 per date) and the upcoming earthworms collected. Termites were sampled with a variety of methods [21]. A complete description of all methods is given in [3].

The classification of functional groups is based on our personal experience with Amazonian fauna and evaluation of the literature. For example, genera of Formicidae were classed as predators, decomposers, herbivores and others. Calculation of biomass for macrofauna was done using size-weight-regressions calculated for each group based on especially sampled material, in some cases by using factors based on measurements of size classes (ants and termites), direct weighing (mites, Collembola) or simple factors from literature (enchytraeids). Earthworm individuals were directly weighed.

2.3. Decomposition

The importance of the different size classes of the fauna in litter decomposition was studied in two experiments using litterbags of three different mesh sizes (1 cm, 250 µm, 20 µm) filled with a "standard litter" (*Vismia guianensis*). Decomposition rates given here are calculated for the coarse litterbags which allowed access of the whole invertebrate fauna. One litterbag series was started at the end of the dry season in October 1997, the second at the end of the rainy season in April 1998 [3]. Decomposition rates were calculated from non-linear regressions (exponential decay) of the ash-free dry weights at retrieval. Regressions were always highly significant ($p < 0.0001$) and showed high r^2 values (> 0.7) [10]. The content

of every single retrieved litterbag was analysed for C and N with an elementary analyser (elementar Vario EL).

3. RESULTS

3.1. Structure of the soil fauna community

Soil mesofauna abundance was around 25 000 ind. m⁻² and dry biomass around 650 mg. m⁻² in three sites but distinctly higher in one plantation (POA) (*table I*). In all sites the mesofauna was strongly dominated by oribatid mites, which accounted on average for 42 - 59% of all individuals and 58 - 71% of the total mesofauna biomass. Predatory mites were also abundant (7 - 22% of individuals, 13 - 16% of biomass). Collembola accounted for 4 - 5% of abundance and 5 - 8% of biomass in the anthropogenic systems, but for 13% of the individuals and 11% of biomass in the primary forest. Enchytraeidae were more abundant in the primary and secondary forest sites with 23 and 25% of the individuals and 13% of biomass, when compared with the polycultures (15 and 17%; 6 and 8%). In relation to the arthropod macrofauna (sampled with larger soil cores) the mesofauna counted for 83 - 90% of the whole faunal abundance and for 40% of the total biomass in POA and 33% in SEC, but only 22% in POC and 18% in FLO.

Macrofauna abundance and biomass were lower in POA and SEC than in POC and FLO (*table I*). Arthropods were generally more abundant in samples taken in December 1997 and 1998, at the beginning of the rainy season and less abundant in June, at the end of the rainy season.

Predatory arthropods made up between 46 and 53% of the whole arthropod macrofauna, decomposers between 35 and 43%. The most abundant predators in all sites were pseudoscorpions, diplurans, ants and spiders. Ants were most abundant in primary forest (16%), and considerably less in the polycultures (3 and 6%). In the polycultures diplopods dominated the decomposer guild (7 and 9% of all arthropods), whereas termites (Isoptera) were the most abundant decomposers in the primary forest (24%). Ants classified as decomposers made up 7 to 8% of all arthropods.

Decomposer biomass differed strongly between the polyculture plots and the primary forest plot. In the polycultures, termites had a much lower biomass (*table II*) and thus accounted only for 8% in POA and 13% in POC, but for 24% of the arthropod biomass in FLO and 22% of SEC. By contrast, diplopods and isopods dominated strongly in the polyculture plots (Diplopoda: POA 18%, POC 12%; Isopoda: POA 17%, POC 43%), but not in the forest (Diplopoda 8% and Isopoda 11%). The biomass of isopods was especially high in POC (*tables II, III*), due to the high abundance of large individuals of *Circoniscus gaigei* Pearse, 1917 (Scleropactidae) (*table IV*). In contrast, the biomass of isopods was very low in SEC (*table II*).

Earthworms, which were collected with the formol extraction method showed rather low and highly variable abundances. The occurrence of very large earthworms led to high biomass values especially in the primary forest and very high variances in the polyculture plots, where these large earthworms occurred only occasionally (*table II*) [19]. Median biomass of earthworms reached 50% of the biomass of all decomposers in the primary forest, 28% in the second-

Table I. Abundance and dry biomass of meso- and macrofauna in the four study sites.

	POA		POC		SEC		FLO	
abundance (ind. m ⁻²)	mean	sdev	mean	sdev	mean	sdev	mean	sdev
meso	32890	62%	25033	28%	24703	40%	24450	21%
macro	3745	37%	4266	41%	3769	31%	4866	31%
biomass (mg. m ⁻²)	mean	sdev	mean	sdev	mean	sdev	mean	sdev
meso	937	69%	655	29%	679	41%	609	21%
macro	1368	28%	2332	48%	1391	62%	2713	38%

Shown are means over 8 sampling events and standard deviations (sdev) in % of the mean.

Table II. Dry biomass of the most important decomposer groups of the macrofauna in the four study sites.

	POA		POC		SEC		FLO	
biomass (mg. M ⁻²)	mean	sdev	mean	sdev	mean	sdev	mean	sdev
termites	109	111%	304	133%	305	44%	654	24%
diplopods	247	69%	276	59%	107	72%	220	85%
isopods	227	77%	994	81%	34	67%	287	66%
earthworms	397	205%	963	123%	259	80%	1541	68%

Shown are means over 8 sampling events and standard deviations (sdev) in % of the mean.

Table III. Biomass of diplopod taxa (strong differences highlighted).

Taxon	FLO	SEC	POC	POA
Siphonophorida	279.5	29.1	1.9	0.0
Stemmiulida	170.9	36.4	75.0	86.1
Pyrgodesmidae	86.8	95.8	250.0	42.5
Cryptodesmidae	0.0	0.0	63.5	2.3
Glomeridesmida	17.8	7.0	33.5	4.6
Chelodesmidae	0.0	8.9	102.7	214.9
Fuhrmannodesmidae	19.9	44.7	99.5	155.1
Cyrtodesmidae	54.4	48.7	68.3	103.0
Paradoxosomatidae	2.1	4.1	0.0	63.7
Polyxenida	3.5	0.5	20.7	13.6
Polyzoniida	0.0	0.0	0.2	0.9
Haplodesmidae	22.0	2.6	17.3	0.0
Polydesmida indet.	0.7	0.7	7.9	1.6
Oniscodesmidae	0.0	0.0	1.8	0.0
Platyrrhacidae	5.2	6.0	0.0	5.8
unidentified	0.5	0.4	0.0	0.3
Sum	663.3	284.9	742.3	694.5

Values are fresh weight in milligrams per square metres.

Table IV. Abundance of *Circoniscus gaigei* and other isopod species.

	FLO	SEC	POA	POC
<i>Circoniscus</i> sp.	0.7	7.2	44.0	70.0
other isopod species	66.4	10.1	16.6	9.4
total	67.1	17.3	60.6	79.4

Values are the number of individuals per square metres.

ary forest and 22% in the polyculture POC, but only 3% in POA. Nine earthworm species have been collected in total. All of them belong to the mainly neotropical family Glossoscolecidae. The most conspicuous worms (up to 110 cm long) belong to *Rhiodrilus contortus* Cernovskov, 1938 and *R. priollii* Righi, 1967. Both species seem to be endemic to the Manaus region. Two other species found in all plots (*Andiorrhinus amazonicus* Michaelsen, 1918 and *Urobenus brasiliensis* (Benham, 1887)) are widely distributed in Amazonia. The smaller species (*Pontoscolex vandersleeni* Michaelsen, 1933 and the new species *Cirodrilus righii* Zicsi et al., 2001 [29]) were only found in few individuals and only in Berlese samples. The circumtropical peregrine species *Pontoscolex corethrurus* (Müller, 1857) was found in all plots except in the primary forest.

In most cases the macrofauna was sorted to higher taxa representing functional groups. Only few taxa were classified to genera and morphospecies. In general, their diversity was lower in the polycultures compared to the primary forest. 42 genera of ants were identified from the primary forest plot, 35 genera from the secondary forest plot and 28 genera from both polyculture plots [10]. The same trend was found in termites (13 genera in FLO, 9 in SEC, 8 in POA and POC). Some taxa common in the primary forest were

never found in the polyculture plots, like Palpigradi and scorpions (Arachnida), most mygalomorph spider species and some ant and termite genera [10]. Great differences in the relative abundance and biomass between primary forest samples and polyculture samples were observed in spiders and especially in the primary decomposer groups Diplopoda and Isopoda (tables III, IV).

In the course of our field studies we found five non-autochthonous diplopod species, originating from Asia, *Trigoniulus corallinus* (Gervais, 1847), *Rhinotus purpureus* (Pocock, 1894); *Asiomorpha coarctata* (Saussure, 1860), or probably introduced by man from other neotropical regions, *Epitrigoniulus cruentatus* (Brolemann, 1902) and *Xenobolus carnifex* (Fabricius, 1775). A few individuals of these species have been found in the polycultures, but never in the primary forest. These exotic diplopod species seem to be especially numerous outside the forests e.g. in pastures, other agroforestry systems and in house gardens.

Strong shifts in species composition and dominance were also found in isopods. These important decomposers were more abundant in POC and FLO than in POA and especially in SEC. In the primary forest plot Philosciidae dominated, whereas *Circoniscus gaigei* Pearse, 1917 was rare. This large body sized scleropactid isopod strongly dominated by abundance and biomass in the polycultures (table IV). It seems to be especially abundant in many other anthropogenic habitats, probably being one of the most important species among the decomposers in man-made landscapes in Amazonia.

3.2. Function of the soil fauna in decomposition

The litterbag experiments clearly showed that the macrofauna determines the decomposition process in all studied plots. When faunal activity was not restricted (coarse mesh), decomposition rates were between 0.6 and 1.4 (kg year⁻¹) in the three anthropogenic sites and 2.3 and 3.1 in the primary forest (figure 1). In the medium litterbags (250 µm), where macrofauna was excluded, decomposition rates were significantly lower (0.3 - 0.6). Further exclusion of the mesofauna in the fine mesh bags did not lower these decomposition rates further [10]. This indicates a strong driving effect of the macrofauna, which cannot be compensated even by an abundant mesofauna. The effect of excluding the macrofauna was strongest in the primary forest where arthropod macrofauna and earthworms were more abundant than in the polycultures and the secondary forest (table II, figure 1). Significant positive correlations with decay rates were calculated for decomposer biomass (including macrofauna arthropods and earthworms) for the first and over both series of litterbag experiments ($p < 0.001$); for earthworms for the second and over both series ($p < 0.001$) and for the total macrofauna for the first series ($p < 0.007$).

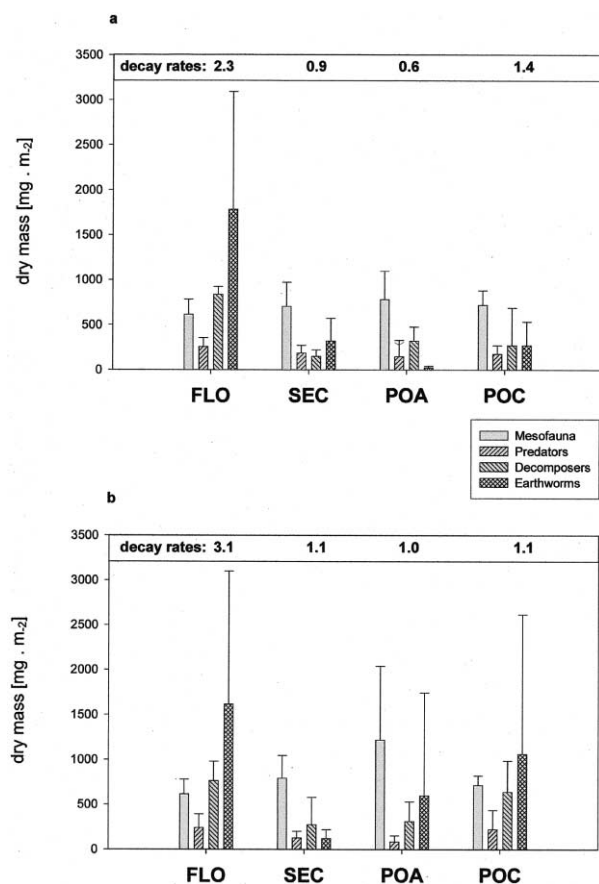


Figure 1. Soil fauna biomass (means and standard deviations) and decomposition rates during the periods of the two litterbag experiments; **a.** first experiment (October 1997 - October 1998); **b.** second experiment (April 1998 - April 1999). Mesofauna comprises both predators and decomposers.

Differences in N-content and C/N-ratio between mesh sizes over all areas were highly significant ($p < 0.001$). Litter exposed in bags with coarse mesh size had a higher relative N-content (1.5%) and lower C/N-ratio (34) as litter in bags where macrofauna and mesofauna were excluded (N 1.1-1.3%, C/N 40). In multiple comparison only differences between coarse and medium and coarse and fine mesh size were significant (both with $p < 0.01$). Within the single areas, differences were significant in POA and POC ($p < 0.05$).

4. DISCUSSION

The identification of the macrofauna showed a substitution of taxon and functional groups in the polyculture plots when compared to primary forest. Here, social insects (mainly termites) and earthworms occurred in high abundance and biomass, whereas in the polycultures other decomposer groups like isopods and diplopods became dominant. Strong shifts were

also observed within the groups, e.g. on the family, genus or species level. Species richness of several predator and decomposer groups was lower in the polyculture systems and the secondary forest, as compared to the primary forest.

Soil and litter inhabiting fauna depends on litter quantity [9] and quality and on microclimatic conditions in the specific habitat, and some of the differences between primary forest and anthropogenic sites shown here are explainable by different abiotic conditions. The decrease of termites and ants in abundance, biomass and diversity may be caused by the distinctly lower stocks of large wood litter in all three anthropogenic plots [10]. On the other hand the decomposer fauna also influences litter quantity and quality of soil organic matter. We hypothesize that the impoverished macrofauna in the secondary forest plot led to the observed litter accumulation in this site [10]. The differences in soil fauna density and decomposition activity between the two plantations might be explained by the more extreme microclimatic conditions (i.e. higher surface temperatures) in one of the plots (POA) [10] and point to the importance of soil covering and shading. Our findings corroborate the hypothesis that tolerance of secondary vegetation in plantations, although creating competition with the culture plants, has positive effects on microclimate and litter layer and, consequently on soil fauna, soil structure and nutrient recycling. These effects seem especially important for low input systems on the extremely poor soils in Amazonia.

Macrofauna biomass (including arthropods and earthworms) in the plots was positively correlated with decomposition rates and negatively with litter stocks. These plot-based results are corroborated by the litterbag experiments, where decomposition rates were much lower in litterbags when macroarthropods have been excluded.

A similar litterbag experiment (three mesh sizes, using *Vismia*-leaves), realized in three other cultivations within the experimental area, a rubber tree monoculture, a peachpalm monoculture and a polyculture with Cupuaçu (*Theobroma grandiflorum*), peachpalm (*Bactris gasipaes*), Brazil nut (*Bertholletia excelsa*) and Urucum (*Bixa orellana*), showed the same effect of the treatments, namely a decrease of decomposition rates by exclusion of the macrofauna [13].

Significant contributions of soil macrofauna to the decomposition of leaf litter in tropical forests in litterbag experiments have already been recorded [1, 23, 28], but in our case they were very high when compared to the effects of the mesofauna. Mesofauna biomass was not correlated with decomposition rates and litter stocks, and exclusion of mesofauna in litterbags did not result in further decrease of decomposition rates. These functional groups seem to play another role in decomposition than the macrodecomposers. The latter accelerate physical and chemical decay by fragmenting large organic particles like leaves and wood and by inoculating the organic

matter with fungal spores during the gut passage. Traditionally, the importance of the mesofauna, which is mainly mycophagous, is seen in their grazing effect, exerting control on microorganismic populations [2].

Positive effects of macrofaunal activity are shown by higher nitrogen content and lower C/N-ratios in the coarse litterbags in all plots. Soil samples from the primary forest, which had the highest macrofauna biomass, showed higher carbon, nitrogen and water contents than samples from the secondary forest and from the polyculture plot in block A [10].

Changes in arthropod communities following deforestation and subsequent land use are well known [7, 8, 18, 26]. However the highest negative effects on soil fauna are caused by ploughing and high grazing pressure. Where a diverse vegetation is established after abandonment of agriculture or forestry, and a litter layer is restored a soil arthropod community can recover [17]. This certainly has occurred in the case of our polyculture tree plantations since they were burned and prepared in 1992.

Summarising our results, we found that the soil fauna in the studied plantation plots still resembles the fauna of the nearby primary forest and, despite structural differences (i.e. in species and dominance spectrum) reaches comparable level of functional efficiency (i.e. concerning litter decomposition).

Acknowledgements. The studies were conducted as part of the SHIFT program based on the German-Brazilian government agreement. They were financially supported by the German Bundesministerium für Bildung und Forschung (BMBF grant nr. 339675) and the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

REFERENCES

- [1] Anderson J.M., Proctor J., Vallack H.W., Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. 3. Decomposition processes and nutrient losses from leaf litter, *J. Ecol.* 71 (1983) 503–527.
- [2] Beck L., Höfer H., Martius C., Römbke J., Verhaagh M., *Bodenbiologie tropischer Regenwälder*, *Geographische Rundschau* 1/1997 (1997) 24–31.
- [3] Beck L., Höfer H., Martius C., Garcia M.B., Franklin E., Römbke J., Soil fauna and litter decomposition in primary and secondary forests and a polyculture system in Amazonia - study design and methodology, *Proc. III. Workshop SHIFT*, Manaus, Brazil, BMBF, Bonn (1998) 463–469.
- [4] Denich M., Kanashiro M., Potential land-use and management of altered and abandoned areas in the Brazilian Amazon region, *Studies of Human Impact on Forests and Floodplains in the Tropics*, MCT/CNPq, Brasília, 1998.
- [5] Dos Santos A.A., Salati E., How research can contribute to the sustainable use of Amazon, in: Lieberei R., Reisdorff R., Machado A.D. (Eds.), *Interdisciplinary Research on the Conservation and Sustainable Use of the Amazonian Rain Forest and its Information Requirements*, CNPq, Brasília, 1998, pp. 20–22.
- [6] Fearnside P.M., Rankin J.M., Jari and development in the Brazilian Amazon, *Interciencia* 5 (1980) 146–156.
- [7] Giller K.E., Beare M.H., Lavelle P., Izac A.M.N., Swift M.J., Agricultural intensification, soil biodiversity and agrosystem function, *Appl. Soil Ecol.* 6 (1997) 3–16.
- [8] Hanagarth W., Überschwemmungsgebiete im peruanischen Amazonasgebiet als Faunenquelle für Agrargebiete, *Amazoniana* 8 (1983) 111–128.
- [9] Höfer H., Martius C., Beck L., Decomposition in an Amazonian rain forest after experimental litter addition in small plots, *Pedobiol.* 40 (1996) 570–576.
- [10] Höfer H., Martius C., Hanagarth W., Garcia M., Franklin E., Römbke J., Beck L., Soil fauna and litter decomposition in primary and secondary forests and a mixed culture system in Amazonia, Final report of SHIFT project ENV 52, BMBF, Bonn, 2000.
- [11] Irion G., Junk W.J., Mello J.A.S. de, The large central Amazonian river floodplains near Manaus. Geological, climatological, hydrological and geomorphological aspects, in: Junk W.J. (Ed.), *The central Amazon floodplains*, Springer, Heidelberg, 1997, pp. 23–46.
- [12] Klinge H., Rodrigues W.A., Bruenig E., Fittkau E.J., Biomass and structure in a Central Amazon rain forest, in: Golley F.G., Medina E. (Eds.), *Tropical ecological systems*, Springer, New York, 1975, pp. 115–122.
- [13] Kurzatkowski D., Streuabbau und Bodenmikroorganismen-Aktivität auf drei agroforstlichen Versuchsflächen in Zentralamazonien (Monokulturen von *Bactris gasipaes* und *Hevea brasiliensis* sowie Mischkultur aus vier Baumarten), *Magisterarbeit*, Universität Göttingen, 1999.
- [14] Lavelle P., Bignell D., Lepage M., Wolters V., Roger P., Ineson P., Heal O.W., Dhillon S., Soil function in a changing world: the role of invertebrate ecosystem engineers, *Eur. J. Soil Biol.* 33 (1997) 159–193.
- [15] Lavelle P., Dangerfield M., Fragoso C., Eschenbrenner V., Lopez-Hernandez D., Pashanasi B., Brussaard L., The relationship between soil macrofauna and tropical soil fertility, in: Woomer P.L., Swift M.J. (Eds.), *Tropical Soil Biology and Fertility*, John Wiley-Sayce, New York, 1994, pp. 137–169.
- [16] Lieberei R., Gasparotto L., Agroecological profile of plants used as production factors and as management components in tropical polyculture systems, *Proc. III. Workshop SHIFT*, Manaus, Brazil, BMBF, Bonn (1998) 307–312.
- [17] Loranger G., Ponge J.F., Blanchart E., Lavelle P., Influence of agricultural practices on arthropod communities in a vertisol (Martinique), *Eur. J. Soil Biol.* 34 (1998) 157–165.
- [18] Römbke J., Verhaagh M., About earthworm communities in a rain forest and an adjacent pasture in Peru, *Amazoniana* 12 (1992) 29–49.
- [19] Römbke J., Meller M., Garcia M., Earthworm densities in central Amazonian primary and secondary forests and a polyculture forestry plantation, *Pedobiol.* 43 (1999) 518–522.

- [20] Serrão E.A.S., Toledo J.M., The search for sustainability in Amazonian pastures, in: Anderson A.B. (Ed.), *Alternatives to Deforestation: Steps towards sustainable use of the Amazon rain forest*, Columbia University Press, New York, 1990, pp. 195–214.
- [21] Silva E.G., Martius C., Termite sampling from soil: Handsorting or Kempson extraction ? *Sociobiol.* 36 (2000) 209–216.
- [22] Teixeira T.D., Leite C.A.M., *Small-scale farmers in the Amazon region of Brazil*, University of Viçosa, 1991.
- [23] Tian G., Kang B.T., Brussaard L., Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions - decomposition and nutrient release, *Soil Biol. Biochem.* 24 (1992) 1051–1060.
- [24] Tian G., Adejuyigbe C.O., Adeoye G.O., Kang B.T., Role of soil microarthropods in leaf decomposition and N release under various land-use practices in the humid tropics, *Pedobiol.* 42 (1998) 33–42.
- [25] Uhl C., Nepstad D., Buschbacher R., Clark K., Kauffman B., Subler S., Studies of ecosystem response to natural and anthropogenic disturbances provide guidelines for designing sustainable land-use systems in Amazonia, in: Anderson A.B. (Ed.), *Alternatives to Deforestation: Steps towards sustainable use of the Amazon rain forest*, Columbia University Press, New York, 1990, pp. 25–41.
- [26] Verhaagh M., Clearing a tropical rain forest - effects on the ant fauna, in: Erdelen W., Ishwaran N., Müller P. (Eds.), *Tropical Ecosystems: Proceedings of the International and Interdisciplinary Symposium Weikersheim, Margraf*, 1991, pp. 59–68.
- [27] Vlek P.L., Serrão E.A., Fölster H., Secondary forests and fallow vegetation in the Eastern Amazon region - a brief overview of the project approach. *Proc. II. SHIFT-Workshop, Manaus* (1998) 45–48.
- [28] Yamashita T., Takeda H., Decomposition and nutrient dynamics of leaf litter in litter bags of two mesh sizes set in two dipterocarp forest sites in Peninsular Malaysia, *Pedobiol.* 42 (1998) 11–21.
- [29] Zicsi A., Römbke J., Garcia M., Regenwürmer (Oligochaeta) aus der Umgebung von Manaus (Amazonien). *Regenwürmer aus Südamerika* 32, *Rev. Suisse Zool.* 108 (2001) 1–12.