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Feeding activities of soil organisms at four different forest sites in Central Amazonia using the bait lamina method

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Abstract: A recently developed technique in soil ecology is the use of the bait lamina method, for assessing the feeding activity of soil animals in situ. Here the bait lamina method (slightly adapted to tropical conditions) was used for the comparison of four closely situated sites (a primary rain forest, a secondary rain forest and two mixed-species tree plantations) in the Brazilian Amazon (project SHIFT ENV-52). The total feeding activity (portion of empty apertures in a set of laminae) and the vertical distribution of the feeding activity were evaluated for differences between the sites. The feeding activities in the primary and secondary forest were at the same level and significantly lower than in the two plantations. Feeding activity in subplots where surface litter has been experimentally removed was significantly lower than in the controls with the litter layer intact, at all four sites. The abundance of soil macrofauna or Enchytraeidae was not correlated with the results of the bait lamina tests, while the abundance of mesofauna (probably mainly Oribatida) was consistent with the pattern of feeding activity. The feeding activities as determined with bait laminae did not correlate with the decomposition activities determined with litterbags. Due to the easy applicability in combination with its feasibility for statistical evaluation and its consistent responses to site differences in experimental treatments we consider the bait lamina method to be a promising approach for the biological assessment of tropical soils.

Key Words: bait lamina test, decomposition, feeding activity, soil fauna, tropical forest

INTRODUCTION

The bait-lamina test is a new approach to assessing functional parameters in soil ecology. With this method the feeding activity of soil animals is measured in situ (Kratz 1998, Von Törne 1990a, b). Bait laminae are small perforated plastic strips that are inserted into the soil. An artificial mixture or natural organic material (= bait) is exposed to soil organisms (e.g. earthworms, Collembola, Diplopoda, Enchytraeidae) in the apertures of the strip. In principle, the loss of the bait material is assessed (Helling *et al.* 1998) by counting the empty apertures after a certain exposition time. The number of empty apertures (i.e. areas from which the bait material has been removed) as well as their vertical distribution are evaluated, and it is assumed that this reflects the feeding activity of soil animals. In addition to measures such as microbial respiration or decomposition activities, feeding activity is thought to be one of several functional parameters applicable for the assessment of the biological status of soils (EA 2003).

The important advantage of the bait-lamina method is its simplicity. Nearly no training, special skill or equipment is necessary. In contrast to the measurement of other functional parameters (like organic matter breakdown determined in a litterbag test), the bait-lamina method does not disturb the soil substrate, needs only short exposure periods (few days up to few weeks) and is rapidly evaluated. As environmental conditions such as climate or soil moisture are expected to strongly influence the results (Kratz & Pieper 1999), the method should only be applied for comparing the biological activity between closely situated plots. In temperate regions, the

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applicability and usefulness of the bait-lamina test for the comparison and assessment of the influence of land use or chemicals on the feeding activity of soil communities has been demonstrated several times (Geissen & Brümmer 1999, Paulus *et al.* 1999). However, bait-lamina tests have so far only once been applied in the tropics (Geissen *et al.* 2001).

The overall aim of this study was to evaluate whether, in addition to established ecological methods, bait-lamina tests are useful for the biological assessment of tropical forest soils. This research is part of the German–Brazilian SHIFT Project ENV-52, which focused on the recuperation of degraded land for sustainable use in Amazonia, Brazil (Höfer *et al.* 2001). In this project the soil communities and – especially – their ecological functions in three different forest types (primary rain forest, secondary forest and plantation) were compared. In parallel to structural (e.g. biomass of soil invertebrates) and established functional parameters (e.g. decomposition of organic matter, microbial respiration), bait-lamina tests were used in order to answer the following questions: (1) Does this method need modification for tropical conditions? (2) Do feeding activities differ between different forest sites (primary forest, secondary forest, forestry plantation), which are known to differ in soil macro- and mesofauna density? (3) Does the removal of the litter layer have any effect on the feeding activities in the soil? (4) Are the feeding activities correlated with decomposition activities (measured by the litterbag method using bags with different mesh size which were filled with *Vismia guianensis* leaves exposed for 1 y) and with abundance or biomass of litter and soil invertebrates in the different forest sites? The first three questions are addressed in this paper. Published data are used to answer question 4 (Hanagarth *et al.* 2004, Höfer *et al.* 2001, Kurzatkowski *et al.* 2004).

STUDY SITES

The campus of the Brazilian research institute Embrapa-Amazônia Ocidental where this study was carried out is situated in central Amazonia, about 30 km outside Manaus (02°53′S, 59°59′W, 100–120 m asl). The natural vegetation is dominated by a dense primary lowland rain forest (terra firme) on nutrient-poor soils classified as yellow clayey latosol (FAO/UNESCO 1997: xanthic Ferralsol); 60% clay, 25% sand; 15% silt; pH 4.0; organic C: 2.5–4.5 %; total N 0.2–0.3%); for details see Martius *et al.* (2004a).

According to Köppen's classification (Heyer 1988, Schröder 2000) the climate in the study region corresponds to the Af-type (A = mean temperature of all months over 18 °C; f = monthly precipitation over 60 mm). Over 30 y (1971–2000) the average annual rainfall was 2554 mm (SD ± 273). The average climate conditions are characterized by a very strong wet season with over 200 mm mo^{-1} rainfall from December to May and a short dry (or low rainfall), but not arid, season from July to September when the prevailing monthly precipitation is still slightly over 100 mm. Average monthly temperatures varied between 25 and > 28 °C with a 30-y mean of 26.0 °C (SD ± 0.9) (Hanagarth *et al.* 2004).

The study sites were 40 × 40-m areas in two forest sites, a primary forest (FLO), a secondary forest (SEC) growing since 1984 and two sites of the same type of forestry plantation (POA and POC, each 32 × 48 m), representing a sequence from undisturbed sites to sites used by man. The forestry plantation was part of a large field experiment with different plantations, where, in 1992, four different tree species of commercial use (*Hevea* spp. (Euphorbiaceae), *Schizolobium amazonicum* (Caesalpiniaceae), *Swietenia macrophylla* (Meliaceae), *Carapa guinanensis* (Meliaceae)) have been planted in rows. In these sites the tolerated secondary vegetation (mainly *Vismia* spp., Guttiferae) was never removed; it dominated the stand and especially the litter production (Hanagarth *et al.* 2004, Höfer *et al.* 2001, Martius *et al.* 2004a). Therefore these plantations are similar to enriched young secondary forests. All sites were situated within a distance of less than 500 m from each other.

The microclimate in the sites showed some strong differences. Mean litter temperatures in FLO, SEC and one plantation (POC) were similar at 25.6–25.8 °C, but in the other plantation (POA) the means were consistently about 1 °C higher. These differences were even more pronounced (up to 2 °C) in very hot years such as 1997. Mean temperatures in the topsoil were similar in FLO, SEC, POC and POA (on average they differed by less than 1 °C). The microclimatic differences between the two plantation sites are correlated with different structural characteristics of the vegetation cover and shading effects of neighbouring sites (Martius *et al.* 2004b).

METHODS

Bait lamina are plastic strips of 120 × 6 × 1 mm, which have a pointed tip at the lower end. In the lower part (85 mm) of each strip 16 bi-conical holes of 1.5 mm diameter are drilled, which are 5 mm apart from each other. These apertures are filled with bait material. A mixture of cellulose (70%) and bran (30%) powder together with a small amount of activated carbon has been used successfully in many studies performed in temperate regions (Kratz 1998). Bait laminae are often exposed in temperate regions for between 10 and 20 d. The number of 'eaten' bait portions (i.e. apertures from which the organic bait

Figure 1. Investigation site in the secondary forest (SEC) located near Manaus, Brazil. Right: Bait lamina test applied to the soil without (background) and with litter layer. Left: Litterbags with three different mesh sizes from the decomposition study.

material has been removed) is taken as feeding activity, often given in per cent of the total of filled apertures for a group of strips exposed together.

In our study the strips were inserted vertically in the soil in a way that the uppermost aperture was just beneath the soil surface. At the end of the exposure period, which had to be determined for the tropical environment (see pre-test), bait laminae were retrieved from the soil and visually assessed by holding the strips against the light and counting empty apertures. Measurement parameters were the total number and the vertical distribution of empty apertures.

Three experiments were undertaken. Firstly, in a short pre-test in July 1997, 100 bait laminae were exposed in the soil in each of three study sites (FLO, SEC, POA) in order to determine the optimal exposure period under Amazonian conditions. After 2, 4, 6, 11 and 18 d of exposure 20 bait laminae were retrieved and examined.

Secondly, in order to determine potential differences between the four sites, five blocks of bait lamina were exposed in each site (FLO, SEC, POA, POC) at four dates (December 1997, June, September and December 1998) in parallel to samples taken for the assessment of soil faunal biomass (Hanagarth *et al.* 2004). Each block consisted of a group of 16 strips, inserted vertically in the soil in a 4×4 grid within an area of about 30×30 cm, following the design used in studies with bait laminae in Central Europe (Federschmidt & Römbke 1994, Irmler 1998, Von Törne 1990a, b). Feeding activities at the four sites were analysed by analysis of variance (mixed model ANOVA). The objective of this analysis was to identify differences between the four sites. Therefore, date was treated as a random factor. Per cent data were always arcsine-transformed to meet the assumption of normal distribution. Homogeneity of variance was checked using the Levene test. The Tukey HSD test was used as a post-hoc test for multiple comparisons.

Finally, the influence of litter removal on the feeding activity was studied in an experiment repeated four times (once in each site) in June (POA), July (SEC) and September (POC, FLO) 1998 (i.e. within the same season). Each time in ten blocks, 16 bait lamina strips were exposed in each of a pair of plots where the litter layer (depth: about 5 cm at all sites) was removed by hand (Figure 1) in the treatment and left in the control plot. The paired plots were less than 50 cm apart while the distance between the blocks was at least 5 m. The blocks were located at areas of each site which had similar environmental conditions (e.g. thickness of litter layer, distance to the forest edge etc.). In parallel, soil pH and moisture were determined at each plot. Effects of the litter-removal treatment and site were tested with a two-way ANOVA after arcsine-transformation of the per cent data. Effects of the litter removal on the vertical distribution of feeding activity and its interactions with site were tentatively tested in a two-way ANCOVA using the mean portion of empty apertures over all 10 blocks per site (x/160) as dependent variable, site and treatment as categorical variables and

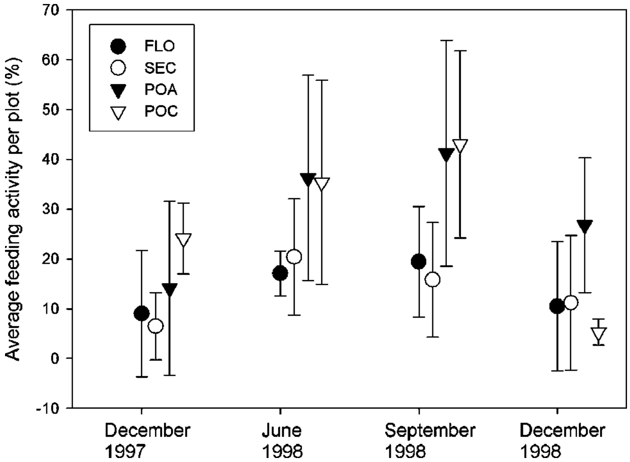

Figure 2. Feeding activity (mean of five blocks per plot ± SD) at the four study sites: primary forest (FLO), secondary forest (SEC) and two forestry plantations (POA, POC), measured as number of fed apertures in per cent of the total number of bait lamina apertures. Sampling was repeated four times between December 1997 and December 1998.

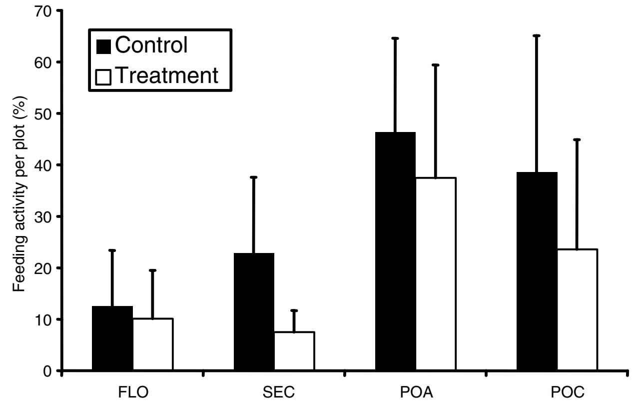

Figure 3. Feeding activity (mean of ten blocks per plot ± SD) in the litter-removal test: Controls versus treatments at the four study sites: primary forest (FLO), secondary forest (SEC) and two forestry plantations (POA, POC), measured as number of fed apertures in per cent of the total number of bait lamina apertures.

depth (hole 1 near surface to hole 16 in *c.* 8.5 cm depth) as covariate.

RESULTS

Pre-test

After 2 d, 27% (FLO) to 70% (SEC) of all filled apertures were found empty. Longer exposure times did not increase the number of empty apertures (i.e. after 18 d 24% (FLO) to 78% (POA) of all apertures were empty). Based on these results we decided to expose the lamina for 4 d in further experiments.

Comparison of the four sites

No other adaptation to tropical conditions except the reduction in exposure time was necessary. However, in the rainy season the combination of clay soil texture and high soil moisture made it difficult to evaluate the feeding activity since the apertures were often filled with mud. In Figure 2, mean values for the total feeding activity at the four study sites are given for all four sampling dates. On average, the feeding activity in the two plantations (POA, POC) was twice as high as in the two forest sites (SEC and FLO). At each sampling date (except in December 1998 at POC), the number of empty apertures was higher in POA and POC compared with SEC and FLO. Also the standard deviation was about twice as high in the plantation sites in comparison with the latter two (Figure 2). After arcsine-transformation of the per cent data the assumptions of normal distribution and homogeneity of variance were met and site had a significant effect on the mean feeding activity ($F_{3,74} = 6.13$, $P = 0.0089$), explaining 20% of the variance in the data. Sampling date explained another 30% of the variance when used as a fixed factor, but did not show any interaction with site. In multiple comparison (HSD procedure) the means at primary (FLO) and secondary forest (SEC) sites both differed significantly ($P < 0.05$) from plantation A (POA), SEC differed also from the other plantation (POC).

Effect of the litter removal treatment

In the litter-removal experiment, the work was performed at three dates but within one season and under comparable environmental conditions. For example, neither the soil pH (4.0 ± 0.2) nor the actual soil moisture (control: 21.3% ± 2.9%; treatment: 21.1% ± 2.8%) differed between the blocks and sites with or without litter layer. Again, feeding activity was significantly higher at POA and POC compared with FLO and SEC (Figure 3; ANOVA: $F_{3,72} = 14.6$, $P < 0.0001$; Tukey HSD: FLO, SEC from POA with $P < 0.001$ and FLO from POC with $P < 0.01$; SEC from POC with $P < 0.05$). At all sites, the number of empty apertures was lower in the plots where the litter had been removed (Figure 3). Notwithstanding the influence of date and site, the effect of the treatment was highly significant ($F_{1,72} = 7.9$, $P = 0.0064$) and similar in all sites (no interaction). Site and treatment explained 43% of total variance.

The vertical distribution of the feeding activity was also different between the sites: i.e. in the top layer more empty apertures were found at POA and POC than at SEC and FLO (Figure 4). An analysis of covariance showed highly significant effects ($P < 0.001$) of treatment ($F_{1,115} = 207$), site ($F_{3,115} = 226$) and depth ($F_{1,115} = 795$) and of the interaction of treatment and site ($F_{3,115} = 36.0$)

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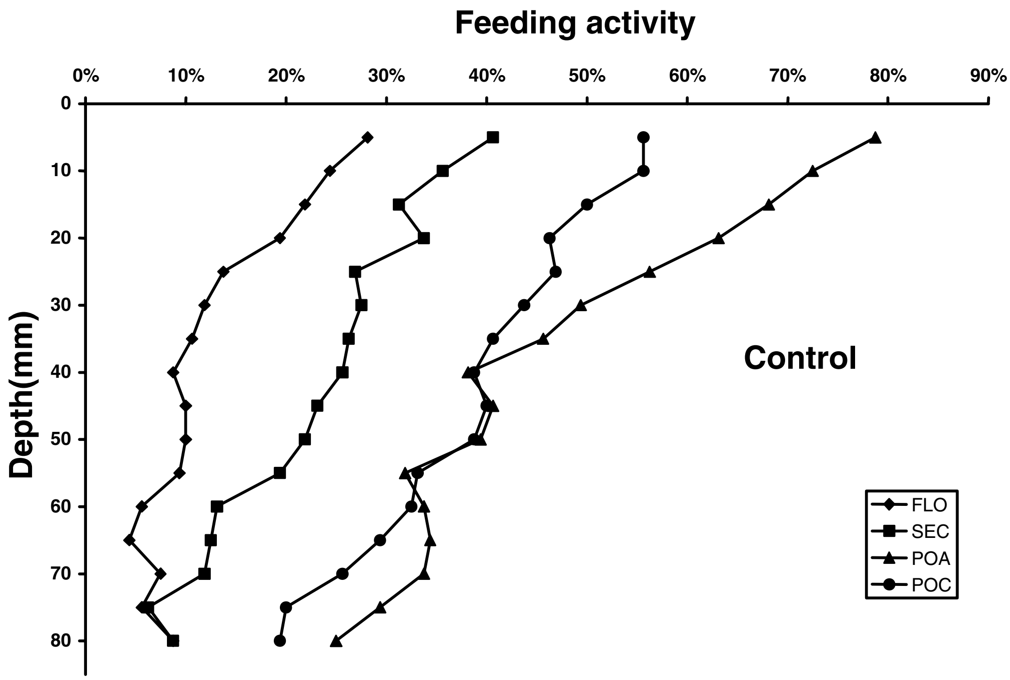

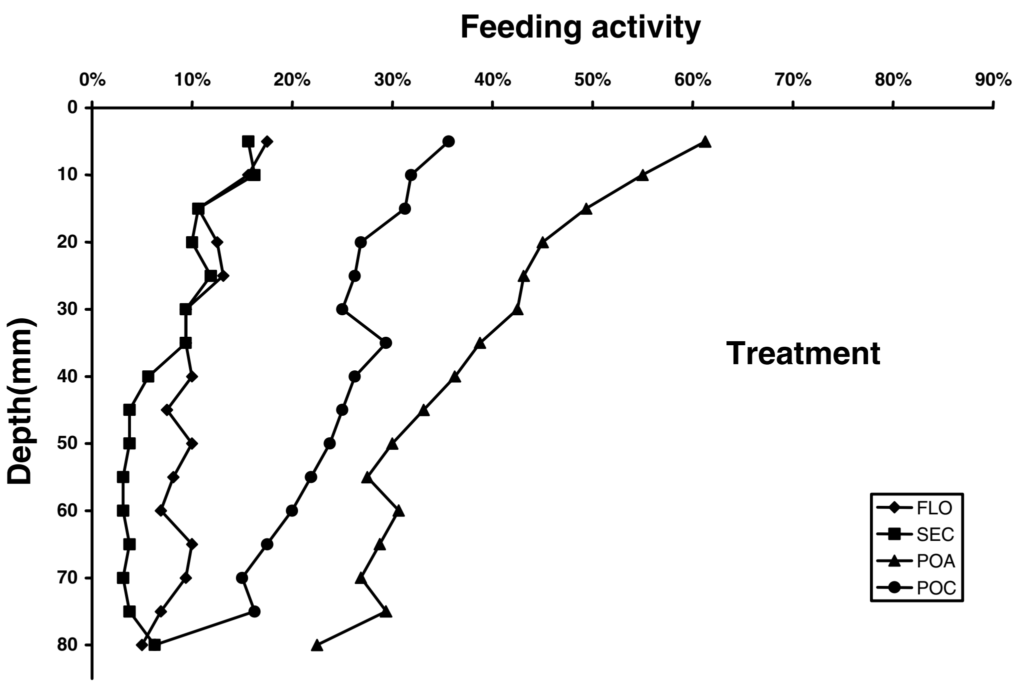

Figure 4. Vertical distribution of the feeding activity in the litter removal test: Controls (upper half) and treatments (lower half). The number of fed apertures per soil depth (0–80 mm) in per cent of the total number of apertures is given for the four study sites (primary forest (FLO), secondary forest (SEC) and two forestry plantations (POA, POC)).

and also for the interaction of treatment with depth ($F_{1,115} = 41.9$) and site with depth ($F_{3,115} = 15.0$). This means that not only the feeding activity but also the distribution of feeding activity along the depth was different between sites and differently influenced by the treatment.

Although strong relations between feeding activities and macrofauna presence were expected, the data on macrofauna abundance and on decomposition from the same sites and period do not fully support this expectation (Franklin *et al.* 2001, Höfer *et al.* 2001). Low feeding activities were observed (and expected) in the

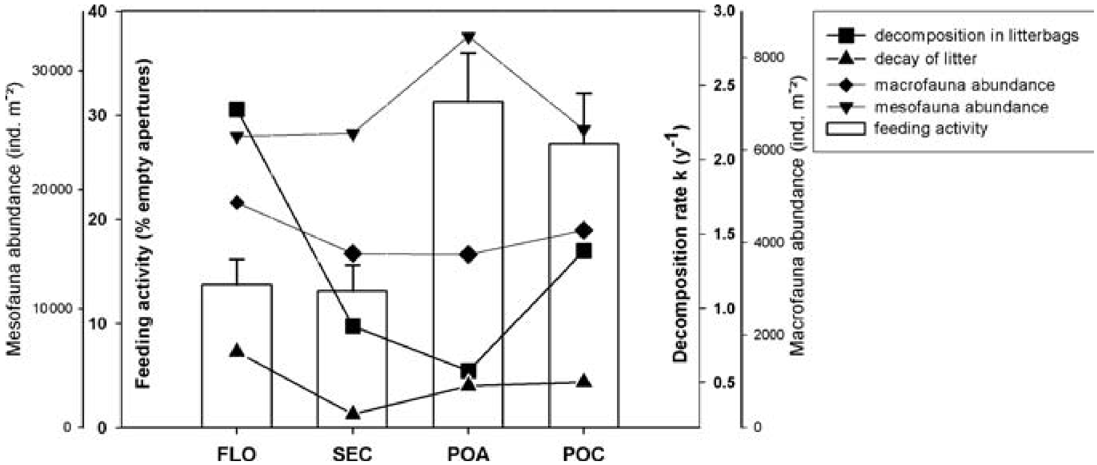

Figure 5. Comparison of functional parameters (i.e. feeding activity, measured with bait lamina and organic matter decomposition, measured with litter bags and as decay of litter stocks) and structural parameters (meso- and macrofauna abundance) at the four study sites: primary forest (FLO), secondary forest (SEC) and two forestry plantations (POA, POC). Feeding activity is given on the left inner axis as empty apertures in %, mean from four dates. Decomposition activities were measured with two different methods (right inner axis: k per year); data from Höfer *et al.* (2001) and Martius *et al.* (2004a). Mesofauna and macrofauna abundance are expressed on the left and right outer axes as ind. m^{-2}.

secondary forest site, where macrofauna (e.g. the social insects: ants and termites) was strongly reduced in abundance and biomass, when compared with the neighbouring primary forest. But in the primary forest site, where the macrofauna community was much more abundant (and diverse), feeding activities were equally low. Much higher feeding activities were observed in plantations, which were similar in vegetation structure and litter production, but differed considerably in their colonization by macrofauna (total macrofauna, as well as all decomposer groups) and in the decomposition of the litter (Höfer *et al.* 2001). Thus, the observed differences in feeding activities between sites cannot be explained by the soil macrofauna (Figure 5).

In contrast, total abundance of mesofauna showed a pattern across the sites similar to the feeding activity, e.g. the highest value at plantation site A and low feeding activities at the primary and secondary forest site (Figure 4; data from Höfer *et al.* 2001). From the three taxa differentiated within the arthropod mesofauna (Oribatida, other Acari, Collembola), oribatid mites dominated strongly in abundance and biomass and were the only group showing the highest value at plantation site A and low values at the primary and secondary forest sites (Franklin *et al.* 2001). Among non-arthropod mesofauna Enchytraeidae (sampled by wet extraction) did not show significant differences in abundance or biomass between sites.

DISCUSSION

The bait lamina test is thought to be an easily applicable and low-effort screening method to assess the feeding activity of soil organisms. Based on our experiences in Amazonian forests and plantations the bait lamina method proved to be applicable in tropical soils. After a slight adaptation of the exposure time the method allows the rapid measurement of site-specific feeding activities, enabling fast repetition and sufficient replication. In addition, it consumes relatively little manpower for preparation and field work. Statistical analysis of the design was straightforward and revealed reproducible differences between the studied sites. In the only other bait lamina test performed in the tropics before, feeding activities of the same order of magnitude as reported here for Amazonian rain forests (10–20% after 14 d) as well as effects of land use were found in savannas of Benin (Geissen *et al.* 2001).

In Europe, macrofauna, in particular earthworms, are thought to be responsible for the removal of the offered bait material (Förster *et al.* 2004). However, at several sites as well as in laboratory experiments the influence of mesofauna groups like enchytraeids and in particular, microarthropod groups like Collembola and mites was shown (Helling *et al.* 1998, Kratz 1998). We hypothesize that oribatid mites may be mainly responsible for the measured feeding activity in the soils of Amazonian forest ecosystems. This hypothesis would explain the failure of a correlation of the observed feeding activities with the decomposition activities, because litterbag experiments in these systems have already shown, that the decomposition activities were controlled by macrofauna and not by mesofauna (Höfer *et al.* 2001, Kurzatkowski *et al.* 2004).

Most of the oribatid mites were extracted from the litter fraction of the soil core samples (Franklin *et al.* 2001) and consequently the decrease of the feeding activities in plots where the litter was removed from the surface could be explained by the disappearance of a large portion of the potential feeders. However, negative microclimatic effect of the removal of litter from the soil surface on density, distribution or activity of the soil fauna could also be expected (Martius *et al.* 2004b) and the significant interactions between treatment, depth and site may reflect this. Removal of the insulating litter layer is expected to have a stronger heating and drying effect in the more open site (e.g. POA) than in a site with a closed canopy (e.g. FLO).

The difference in feeding activities between both forest sites and the plantations is surprising. Also, the difference in feeding activities between SEC and POC, which showed similar mesofauna abundances, remains unexplained. Factors other than abundance, such as biomass, might influence the feeding activities. Typical mesofauna food sources (e.g. easily consumable products derived from the primary decomposition through macrofauna) might have been scarce at the two plantation sites POA and POC (Höfer *et al.* 2001). Under such conditions the baits could have been more attractive for hungry soil animals there. Nevertheless the quantity of food introduced with the baits should be negligible in comparison to the amount of organic matter still available at POA and POC. Also some species or species groups (guilds) of meso- or macrofauna might profit more than others and a different species composition at the different plots become visible by the feeding activity. In particular, a few species of isopods and diplopods were much more abundant in the two plantations than in the two forest sites.

Although the causes of the difference between feeding activities and decomposition activities are not clear in detail, we conclude that these two functional measures can both be valuable reflections of the biological conditions of a (tropical) soil. While the ecological relevance of changing decomposition activities for the whole soil ecosystem is not in question (Cadisch & Giller 1997), further research is needed to determine what differences in the feeding activity do mean for the biological status of a particular soil.

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