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Soil Fauna and Litter Decomposition in Primary and Secondary Forests and a Mixed Culture System in Amazonia

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Abstract

This report represents an account of the activities carried out in the second year of the project as well as of the results obtained from the 1997-1998 data and the first series of decomposition experiment with litter bags. Based on the still preliminary results, the study areas can be arranged into a sequence from the primary forest area FLO over one plantation site, POC, to the secondary forest site, SEC, and the second plantation site, POA.

FLO is characterized by a relatively homogenous temperature regime in litter and topsoil, and relatively stable humidity conditions in the litter layer, by a high litter production and low litter stocks. "Ecosystem" litter decomposition rates (as calculated from litter stocks and production) are high. The decomposition rates of *Vismia* litter in the coarse mesh litter bags (macrofauna present) are also high. Nitrogen contents in litter and topsoil are high, and soil carbon is higher than at the other sites. Macrofauna abundances are high, predators and ants dominate, and termites occur very frequently.

On the other end of the sequence, the polyculture area in block A (POA) is characterized by very large temperature and humidity extremes on the ground, by low litter production, low "ecosystem" decomposition rates resulting in the accumulation of larger litter stocks. Decomposition rates in litter bags are also lower, and macrofauna abundance is low, with remarkable high relative abundances of primary decomposer arthropods (Isopoda and Diplopoda), but a low frequency and abundance of ants and termites. The secondary forest area SEC is similar to POA in most aspects; only litter accumulation (stocks) is still higher, and this site has the lowest "ecosystem" decomposition rate of all.

The other two areas range in between, most often the polyculture area of block c POC is more closer in its characteristics to FLO.

Climatic conditions (soil and litter temperature, litter layer air humidity) in the open sites (POA and SEC) show larger extremes than in FLO. In POC, they are clearly less harsh than in POA. We hypothesize that these abiotic conditions control the soil fauna density and functional composition more than the site-specific characteristics (e.g. history, plant system, soil).

The litter bag experiment clearly shows that the macrofauna determined the litter decomposition rates in all areas. When macrofauna was excluded from the litter bags, decomposition rates decreased to 43-46% (70% in POA). Further exclusion of the mesofauna by very fine mesh did not result in lower decomposition rates (although in mini-container experiments, a small influence of the mesofauna was detected). In the

remaining litter, the N concentration increased during the decomposition experiment, more strongly in coarse litter bags and in FLO and POC.

The assessment of macrofauna in the Berlese samples shows a possible substitution of faunal groups between the sites. In FLO, social soil insects (ants, termites) and earthworms have larger individual numbers, whereas in the polycultures, other decomposer groups like isopods and diplopods have higher abundances. However, we have to confirm these trends in terms of biomass.

Soil fauna feeding activity decreased in response to an experimental reduction of litter. However, the relatively small differences in litter input between the sites do not explain the relatively large differences in decomposition rates. We hypothesize that factors like soil microclimate and litter quality (nitrogen content) account for the observed differences.

One aim of the project was to test the applicability of fast assessment methods. Mini-containers, by design, do not allow to assess the role of macrofauna, a serious shortcoming in view of the importance of this group. Bait-lamina results on soil fauna feeding activity were often the completely opposite of the data on fauna density from direct assessments. Further analysis of all data in the context will allow to address these issues further.

Resumo

Este relatório representa um relato das atividades efetuadas no segundo ano do projeto como também dos resultados obtidos dos dados de 1997-1998 e da primeira série de experimentos de decomposição com sacos de liteira (serrapilheira). Baseado nos resultados ainda preliminares, as áreas de estudo podem ser organizadas numa série, começando da área de floresta primária FLO via um dos locais de plantação, POC, até o local de floresta secundária, SEC, e o segundo local de plantação, POA.

FLO é caracterizado por um regime de temperatura relativamente homogêneo em liteira e topsolo, e condições de umidade na camada de liteira relativamente estáveis, por uma produção alta de liteira e baixos estoques de liteira. A taxa de decomposição de liteira "do ecossistema" (calculada baseado nos estoques e produção de liteira) é alta. A taxa de decomposição de liteira de Vismia nos sacos de liteira de malha grossa (macrofauna admitida) também é alta. Conteúdos de nitrogênio em liteira e topsolo são altos, e o teor de carbono no solo é mais alto que nos outros locais. Abundâncias de macrofauna são altas, predadores e formigas dominam, e térmitas ocorrem muito freqüentemente.

No outro fim da série, a área de policultivo no bloco A (POA) é caracterizada por extremos de temperatura e de umidade no solo muito altos, por uma baixa produção de liteira, e uma baixa taxa de decomposição "do ecossistema", resultando na acumulação de maiores estoques de liteira. A taxa de decomposição em sacos de liteira também é mneor, e a abundância da macrofauna é baixa, com abundâncias relativas de artrópodes-decompositores primários (Isopoda e Diplopoda) bastante altas, mas uma baixa freqüência e abundância de formigas e térmitas. A área de floresta secundária SEC é semelhante á POA na maioria dos aspectos; só a acumulação de liteira (estoques) é ainda mais alta, e este local tem a mais baixa "taxa de decomposição do ecossistema" de todas.

As outras duas áreas estão situadas entre estas duas, freqüentemente as características da área de policultivo do bloco C POC são mais similares às de FLO.

Condições climáticas (temperatura de solo e liteira, umidade do ar na camada de liteira) nos locais mais abertos (POA e SEC) mostram extremos maiores que em FLO. Em POC, elas estão claramente menos severos que em POA. Nós hipotetizamos que estas condições abióticas controlam a densidade de fauna de solo e a sua composição funcional mais que as características específicas do local (por exemplo história, sistemas de plantio, solo).

O experimento com sacos de liteira mostra claramente que a macrofauna determina

as taxas de decomposição de liteira em todas as áreas. Quando macrofauna foi excluída dos sacos de liteira, as taxas de decomposição diminuíram em 43-46% (70% em POA). Uma exclusão ainda da mesofauna através do uso de uma malha muito fina não reduziu mais a taxa de decomposição (embora em experiências de míni-container foi encontrada uma pequena influência da mesofauna). Na liteira restante, a concentração de N aumentou durante o experimento de decomposição, mais fortemente nos sacos de liteira com malha grossa em FLO e POC.

A avaliação da macrofauna nas amostras de Berlese mostra uma possível substituição de grupos de fauna entre os locais. Em FLO, insetos sociais habitantes do solo (formigas, térmitas) e minhocas têm números individuais maiores, embora que nos policultivos, outros grupos de decompositores como Isopoda e Diplopoda têm abundâncias mais altas. Porém, temos que confirmar estas tendências em termos de biomassa.

A atividade de forrageio da fauna de solo diminuíu em resposta a uma redução experimental de liteira. Porém, as diferenças na produção de liteira relativamente pequenas entre os locais não explicam as diferenças relativamente grandes nas taxas de decomposição. Hipotetizamos que fatores como o microclima do solo e a qualidade de liteira (conteúdo de nitrogênio) são responsáveis pelas diferenças observadas.

Um objetivo do projeto era testar a aplicabilidade de métodos de avaliação rápidos. Míni-containers, já pelo seu design, não permitem avaliar o papel da macrofauna, uma falta séria em vista da importância deste grupo. Resultados de testes com lâminas-iscas sobre a ativiaded de forrageio da fauna de solo freqüentemente foram o oposto completo dos dados sobre a densidade da fauna tirados de avaliações diretas. Uma futura análise de todos os dados no contexto permitirá entender melhor estes assuntos.

Zusammenfassung

Wir berichten über die Aktivitäten daß im zweiten Jahr des Projektes sowie über die Ergebnisse aus den 1997-1998 erhobenen Daten und aus dem ersten Abbauexperiment mit Streubeuteln. Basierend auf den noch vorläufigen Daten können die Untersuchungsgebiete in eine Sequenz vom der Primärwaldfläche FLO über eine Plantage POC und die Sekundärwaldfläche SEC zur zweiten untersuchten Plantagenfläche, POA, gebracht werden.

FLO wird charakterisiert durch ein relativ gleichförmiges Temperaturregime in Streu und Oberboden, eine relativ stabile Luftfeuchtigkeit in der Streuschicht, hohe Streuproduktion und geringe Streumengen auf dem Boden. Die "Ökosystem"-Streuzersetzungsrate (aus Streuvorräten und -produktion kalkuliert) ist hoch. Die Abbaurate von *Vismia*-Streu in den Streubeuteln grober Maschenweite (Makrofauna präsent) ist ebenfalls hoch. Stickstoffgehalte in Streu und Oberboden sind hoch, und die Kohlenstoffkonzentration im Oberboden ist höher als im Boden der anderen Flächen. Makrofaunadichten sind hoch, Prädatoren und Ameisen dominieren, und Termiten kommen sehr häufig vor.
Am anderen Ende dieser Sequenz steht das Mischkultursystem in Block A (POA), in dem die Bodentemperatur und Luftfeuchte durch sehr große Extremwerte in gekennzeichnet sind, und welches durch niedrige Streuproduktion und niedrige "Ökosystem"-Abbaurate charakterisiert ist, was zur Ansammlung höherer Streuvorräte führt. Die mit Streubeuteln ermittelten Zersetzungsraten sind ebenfalls niedriger, und die Dichte der Makrofauna ist geringen, mit bemerkenswert hohen Anteilen primärer Zersetzerarthropoden (Isopoden und Diplopoden), aber niedrigen Frequenzen und Dichten von Ameisen und Termiten. Die Sekundärwaldfläche SEC ähnelt POA in den meisten Aspekten ähnlich; nur die Ansammlung von Streuvorräten ist höher und diese Fläche hat die niedrigsten "Ökosystem"-Abbauraten von allen.
Die anderen zwei Flächen liegen dazwischen, wobei die Mischkulturfläche in Block C, POC, in den meisten Merkmalen näher an FLO liegt.
Klimabedingungen (Boden- und Streutemperatur, Luftfeuchtigkeit in der Streuschicht) auf den offenen Flächen (POA und SEC) zeigen größere Extreme als in FLO. In POC sind sie eindeutig weniger extrem als in POA. Wir vermuten, daß diese abiotischen Zustände die Bodenfaunadichte und Zusammensetzung der Fauna in Hinblick auf funktionelle Gruppen stärker bestimmen als Flächeneigenschaften (z.B. Nutzungsgeschichte, Pflanzsystem, Boden).
Das Streubeutelexperiment zeigt eindeutig, daß die Abbauraten in allen Flächen von

der Makrofauna bestimmt werden. Wenn Makrofauna aus den Streubeuteln ausgeschlossen wird, nehmen die Zersetzungsraten um 43-46% ab (70% in POA). Ein weiterer Ausschluß der Mesofauna durch sehr feine Maschenweite reduziert die Abbauraten nicht weiter (obwohl in Mini-Container-Experimenten ein geringer Einfluß der Mesofauna beobachtet wurde). In der in den Beuteln verbliebenen Streu nahm die N-Konzentration während des Abbauversuches zu, stärker in groben Beuteln grober Maschenweite und in FLO und POC.

Die Erfassung der Makrofauna in Berleseproben zeigt, daß möglicherweise gewisse Faunengruppen, die in einer der Flächen vorkommen, in anderen Flächen durch andere Gruppen ersetzt sind. Soziale Bodeninsekten (Ameisen, Termiten) und Regenwürmer haben in FLO größere Individuenzahlen, wohingegen in den Mischkulturen andere Zersetzergruppen wie Isopoden und Diplopoden eine höhere Dichte haben. In Hinsicht auf Biomasse müssen diese Trends aber noch durch weitere Auswertung bestätig werden.

Die Fraßaktivität der Bodenfauna verringerte sich in Reaktion auf eine experimentelle Streuverminderung. Aber die relativ geringen Unterschiede im Streufall zwischen den Flächen können die relativ großen Unterschiede in den Abbauraten nicht erklären. Wir vermuten, daß Faktoren wie Boden-Mikroklima und Streuqualität (Stickstoffgehalt) für die beobachteten Unterschiede verantwortlich sind.

Ein Ziel des Projektes war es, die Anwendbarkeit von Schnellerfassungsmethoden zu prüfen. Aufgrund ihres Designs ist es mit Mini-Containern nicht möglich, die Rolle der Makrofauna zu erfassen, ein ernster Mangel angesichts der Bedeutung dieser Faunengruppe. Ergebnisse der Köderstreifentests zur Fraßaktivität der Bodenfauna waren den Daten zur Faunenabundanz oft diametral entgegengesetzt. Erst die weitere Analyse aller Daten im Kontext wird es erlauben, diese Fragen weiter zu erörtern.

1. Introduction

In the project ENV 52, the role of soil fauna and microflora in the nutrient cycles of experimental agro-ecosystems is studied. These systems have been originally designed as an alternative to the conventionally grown annual crops in the Amazon region by project 23 and others.

The project started in October 1996 and, after installing a state-of-the-art soil fauna lab at the Embrapa in Manaus, the field investigations were initiated in June 1997.

In 1998, the largest part of the field program was accomplished. Since September 1997 the joint sampling of microflora, meso- and Makrofauna and earthworms has been realized every three months. Seven of 8 planned sampling events have now successfully been carried out and the resulting material has been processed in the laboratory. The first series of two litter bag experiments with 1008 litter bags exposed in the field were finished in November 1998, and the second series is in the field and retrievals are regularly taking place.

Most of the data have been processed and a first evaluation of data has proceeded quite far, as show the reports by different project participants annexed to this report. Caution should be taken as the results remain preliminary and final conclusions can only be drawn at the end of the project.

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2. The research group

Project Management:

Prof. Dr. Ludwig Beck (SMNK)	German project leader
Dr. Luadir Gasparotto (EMBRAPA-CPAA)	Brazilian project leader
M.Sc. Marcos B. Garcia (EMBRAPA-CPAA)	Brazilian project coordinator, macrofauna, ants
Dr. Hubert Höfer (University Göttingen)	German project coordinator, macrofauna, predator impact, decomposition rates, C/N-analyses
Dr. Christopher Martius (SMNK, now ZEF Bonn)	German project coordinator until June 1998, microclimate, termite and litter studies [was contracted by ZEF in June 1998]
Dr. Werner Hanagarth (SMNK)	replaces Dr. Martius since July 1998, German project coordinator, macrofauna biomass, environmental impact, land use systems

Researchers:

Dr. Bernhard Förster (ECT)	microbial biomass, respiration measures (IRGA)
Dr. Elizabeth Franklin (INPA)	oribatid fauna, litter bag colonization
Dr. Thierry Ray Jehlen Gasnier (University Manaus)	cockroaches
Dr. Ana Harada (Museu Goeldi)	ants
Dr. Flavio Luizão (INPA)	litter bag-experiment
Dr. Regina Luizão (INPA)	microbial biomass
Dipl. Ing. (FH) Chem. Martina Meyer (SMNK)	chemical analyses
Dr. José Wellington de Morais (INPA)	wood litter stocks
Dr. Elisiana Oliveira (INPA)	springtails [left project in March 1998]
Dr. Jörg Römbke (ECT)	oligochaeta fauna (earthworms, enchytraeids)

Students:

Dipl. Biol. Cäcilia Hanne (University Frankfurt)	respiration of termites
M.Sc. Ricardo Ott (INPA)	experimental study of predator impact
M.Sc. Lucilene Gomes da Silva Medeiros (INPA)	food guilds in termites
M.Sc. Everaldo Gomes da Silva (INPA)	abundance and biomass of termites
M.Sc. Maristela Farias (CNPq fellow)	microbial biomass (IRGA)
M.Sc. Maria do Socorro Souza da Mota	Litter experiment (started August 1998)
Yelinda Vergara	Litter experiment/earthworms
Tânia Ferreira Hayek (CNPq fellow)	Mesofauna
Evanira Maria Ribeiro dos Santos (CNPq fellow)	Mesofauna
Edilson Paez Fagundes, (Bolsista PIBIC/CNPq/INPA)	Oribatidae in litter bags

Technicians:

Gessiene do Nascimento Pereira (CPAA)	laboratory technician, animal sorting
Valdinez Ribeiro Montoia (CPAA)	laboratory technician, animal sorting
Francisco Aragão (CPAA)	field worker
Estevão Oliveira dos Santos (EMBRAPA-CPAA)	laboratory technician, C/N-analyses

3. Study Area and Methods

Comparative studies are made in the following study sites, situated within and close to an experimental 19-ha area, divided into 5 blocks (A-E), of the Embrapa-CPAA at km 29 on the road Manaus-Itacoatiara:

- a primary forest (called FLO in the following),
- a secondary forest (SEC) nearby, growing since 1992, which grows in an abandoned former rubber tree monoculture,
- one area of polyculture system 4, a silvicultural plantation of four different tree species, planted in 1992, with secondary vegetation admitted between the tree rows, in block A (POA),
- another area of the same type (system 4), in the block C (POC)

The basic hypotheses of the project and the field design and methods were described in two manuscripts written for the SHIFT-Workshop proceedings (Beck et al. 1998a, b; see list of publications) and all the methods used are compiled and presented in our homepage (http://www.cpaa.embrapa.br/env52).

In our study, the sites are characterized with respect to soils, vegetation, microclimate and litter stocks and production. In an extensive sampling program, soil fauna and microflora biomass and activity are investigated related to these characteristics.

Additionally, some important factors influencing the systems are studied:
1. the effect of experimental increase of litter quantity in areas of 1 m² on microbial biomass, and nutrient (C, N, Ka, Ca, Mg, P) quantity;
2. the effect of increased and decreased number of arthropod predators (spiders) on macro- and mesofauna density and on litter decomposition rates.
3. The effect of an experimental litter increase on soil fauna feeding activity (bait lamina).
These experimental studies test hypotheses about functional responses and will enable to link the parameters measured in the basic sampling program.

In addition to the sites mentioned above, a M.Sc. study (Darek Kurzatkowski, University of Göttingen) on soil respiration and decomposition rates using a litter bag experiment was carried out from May to November 1998 in which the investigations were extended to two other areas of interest:

- a monoculture of peach palm (pupunha; *Bactris gasipaes*) in blocks A and D, characterized by a very closed canopy;

- the plantation system 2, which consists of several fruit trees intersparsed and planted into rows (blocks A and D), a very openly structured system.

4. Project activities in 1998

The "basic sampling program" comprising sampling of microbial biomass and respiration, abundance and biomass of mesofauna, macrofauna, and earthworms was done on 2-3 March, 2-3 June, 1-2 September, and 1-2 December, 1998 (each collection took two days to be accomplished). Four different soil core samples were taken in several replicates at each date: Small cores (6.5 cm diameter) were taken for (1.) respiration measurements, (2.) mesofauna (arthropods) extraction with the Kempson apparatus, and (3.) enchytraeid wet extraction, and large cores (21 cm diameter) were taken for (4.) the macrofauna (arthropods) extraction with the Berlese apparatus.

In each of the three studied systems (primary forest FLO, secondary forest SEC, polyculture system 4 POA and POC) 10 samples for each method were taken at the first day, starting with the polyculture POA and continuing in SEC and FLO. The next day, another 10 samples were taken at each site, this time starting with POC. Thus, in total 20 samples for each method of each system are collected.

Additionally, in every system two (one per day) 4 m² areas were hand-collected for large arthopods. From the same areas earthworms were extracted by formol application.

Litter stocks were sampled with 20 large core samples every month. Litter fall was taken from 20 litter collectors installed per system, sampled every week. Within one month all collected substrates were extracted or dried, weighed and ground for analyses. The very laborious sorting of the extracted meso- and macrofauna took 3-4 months per sampling event.

From the first litter bag series, exposed 27 October 1998, always 14 samples per system and mesh width (totally 126) were retrieved at 7 dates (after 25, 57, 84, 112, 168, 252 and 365 days). All litter bags were visually controlled for fauna, fungi and root penetration. The remaining weight of the leaf material was determined. Subsequently 10 bags of each system and mesh width were used for mesofauna extraction in the Berlese apparatus, 2 bags for enchytraeid extraction and 2 bags for respiration measurements. Leaves were finally ground and the ash-content and C and N-content analysed for every single litter bag (except from third retrieval).

Thirty mini-container bars were exposed in each system together with the litter bags and retrieved at the first three retrieval dates of litter bags. After visual control and drying, the remaining weights were determined and the remaining leaf material was ground and analysed (as mixed samples for area and mesh width).

The second series of litterbags was exposed 22 April 1998 and is processed similarly to the first series, except for an elimination of the retrieval after 3 months for technical reasons. To date four sets were retrieved and processed.

Bait lamina were used on several occasions, (1.) during the days of the basic sampling program, to study soil fauna feeding activity in the sites, and (2.) to study the correlation of fauna feeding activity and litter stocks on a small scale.

5. Summary of Results

Here, only the most important results are summarized. They are detailed in the individual reports in the annex.

5.1 Soils

From a still limited soil data set we draw the preliminary conclusion that both pH and soil moisture are quite similar at all sites. Only the soil at FLO had a higher moisture content. Soil structure is similar at all sites. Relative N concentration was 0.20-0.26% in SEC and POA, and 0.27-0.31 in FLO (POC in between). Carbon concentration varied between 2.5 and 3.5% in SEC and POA, and between 3.6 and 4.5% in FLO (POC again in between). Thus, slightly higher soil organic matter was always found in FLO than in the other sites. The soil at POC which is narrowly adjacent to a primary forest seems to be most similar to the undisturbed forest site. However, the differences are small (Figure 1).

5.2 Climate

From small data loggers on each site, two sets of data have been compiled up to now, one ranging from July 1997 to February 1998, the second from May to November 1998. The interruption of the measurements between February and May was due to technical reasons (battery replacement was necessary). In the first period, average litter temperature ranged from 26.4 to 26.6°C at the sites FLO, SEC, and POC, and was 28.4°C in POA(Table 1). In the second period, it ranged from 25.6 to 25.8°C in FLO, SEC and POC, and again was higher (26.8°C) in POA (Table 2). Soil temperatures at 0-5 cm depth are generally at least 0.2 degrees lower (Table 1) or of less variability than litter temperatures (Table 2). The temperature maxima and humidity minima show that the more open-structured sites, principally POA, are characterized not so much by different average temperatures, but much higher extremes (Tables 1, 2).

Average humidity in the litter layer was generally higher in the second period than in the first. It was always lowest in POA, again indicating that the harshest conditions reigned on this site.

Rainfall data for the period 1996-1998, kindly provided from the Embrapa-CPAA, showed that the average monthly precipitation was 215 and 216 mm/month in 1996 and 1998, respectively, but only 187 mm/month in 1997.

Two conclusions can be drawn from these data:

1 Although the duration of the two measuring periods was not strictly equal, it is

obvious that average temperature was higher and average humidity lower during the first of both, although the rainy season November to February fell in this period. Together with the rainfall data this shows that effects of the 1997 El Niño Southern Oscillation on microclimate in Central Amazonia were considerable.

2 Soil and litter temperatures and air humidity at soil level in the plantation POA were very different from POC. These differences coincide with data on macrofauna abundance, weight loss in litter bags, etc. Temperature maxima in POA by far exceeded those of the other sites, whereas in POC they were close to values in FLO, probably due to the influence of shading from a directly neighboring primary forest.

Similar measurements in the open site of polyculture system II in block B showed the highest average litter layer temperature of 29.7°C, whereas the pupunha monoculture at block C did not differ significantly from the other sites (Table 2). Based on these data, we are able to establish a sequence of increasingly harsh microclimatic conditions for soil biota, from FLO over SEC, Pupunha, POC, POA to System II.

5.3 Litter

5.3.1 Litter Production. The average annual litter production estimated from weekly collections between June 1997 and December 1998 (72 weeks) was highest in the primary forest area (9.5 ± 2.4 t/ha·a). However, the **monthly** litter production of FLO differed significantly only from POA and POC. The monthly values (Figure 2) also show a large variance in litter fall between the seasons of the year. The lowest litter fall was measured at POA (6.7 ± 1.3 t/ha·a), although the difference of the monthly values to POC and SEC is not significant.

Litter production in September 1997 was much higher than in the same period in 1998 (Figure 2). We hypothesize that the prolonged drought period and higher temperatures observed 1997 led to severe stress for the vegetation which reacted shedding more leaves than usual.

5.3.2 Litter Stocks. The weights of the monthly measured litter stocks at SEC almost doubled those of FLO, which where the lowest of all areas. Litter stocks at SEC were significantly higher than those of all other sites (Figure 2).

5.3.3 Litter Decomposition Rates. The highest average monthly litter production in FLO coincided with the lowest average monthly litter stock in this site. This suggested an analysis of decomposition rates, and we pooled the monthly litter production (data from the last 4 weeks before a litter stock assessment) and divided it by the respective value of litter stocks in order to obtain an indicator of the velocity of the decomposition process at each site (Figure 2). Values were highest at FLO, and significantly different from SEC, POA and POC. The lowest decay rates were calculated for SEC. This means that in terms of decomposition rate, the polyculture areas were far different from the primary forest area in our studies, a result with important implications for the evaluation of the decay processes in these sites. However, the decay rates at SEC were still lower.

5.4 Microbial Biomass and Respiration

The overall microbial biomass in the upper soil layer appeared to be low compared with data from forest soils of the temperate zone. Respiration in litter exceeded the soil respiration by a factor of up to 100. The potential respiration and biomass in soil samples from the different areas [at all sites and during the course of the year] did not present significant differences during the study period. Therefore, with respect to microorganisms, the potential of the sites seems quite similar. Different microclimatic conditions, however, e.g. soil moisture and temperature, may lead to different real soil respiration rates at the sites. Differences in weight loss (see below) under exclusion of soil fauna through fine-mesh litter bags point to a different microbiological activity in the different areas (lowest in SEC and POA).

5.5 Fauna

5.5.1 Mesofauna. Due to the time-consuming sorting process needed for the analysis of this faunal group (defined as animals of less than 1 mm body diameter, extracted in the Kempson apparatus), only data for the first three sampling events (July to December 1997) are available for this report. Mesofauna density in the soil fraction of the samples was always higher than in the litter fraction. No clear differences between the sites appear in this data set. Litter mesofauna density of the sites was almost similar (exception: in September, density in FLO was much higher than in SEC and POA/POC), whereas the soil mesofauna abundances in FLO and POA/POC were significantly higher than in SEC. Acari:Oribatida (20-53%), other Acari (13-33%) and Collembola (4-12%) were the most dominant groups. The highest taxa diversity was found in samples from FLO, followed by SEC and POA/POC. The low density values in the hottest month, July 97, point to the effect of drought, in 1997 possibly further enhanced by the El Niño effect.

5.5.2 Enchytraeidae. Due to the live extraction process needed to identify enchytraeids, data are available for all collections 07/97 to 06/98. Twenty out of the 24 enchytraeid species found up to now are new to science. In many samples their density in the soil layer is higher than in the litter layer. First data indicate that the number of enchytraeids is highest at the end of the rainy season (June/July). No difference in individual numbers between the areas can be discerned from the preliminary data set. Individual numbers range from 1600 to 8000 individuals/m^2, corresponding to a very low (estimated) biomass in the range of 200-4000 mg/m^2. Based on these data, we consider the quantitative role of this group of soil fauna in the decomposition process to be less relevant.

5.5.3 Macrofauna. This section refers to the arthropods extracted from soil cores with the Berlese apparatus. Earthworms are treated in the following section. Although termites from Berlese have been included analyses, additional studies of nest-building and soil-dwelling species are reported below.

During the studied interval (July 1997 to June 1998), the total abundance of all arthropods, extracted from the soil cores of 21 cm diameter with the Berlese apparatus, decreased slightly, but continuously in almost all sites (Figure 3). However, this trend is mainly due to the high, but decreasing abundance of predators (principally Pseudoscorpiones). The relative number of decomposers is much lower and did not decrease during this period. In FLO and SEC, their abundance even increased. In POA and POC a large number of decomposers was observed in December 1997, at the beginning of the rainy season (Figure 4).

Ants and termites were much more abundant and more frequent in the primary area FLO than in the other sites. Particularly termites occurred only sporadically in the plantation sites POA and POC. On the other hand, the abundance of other decomposers, particularly Isopoda and Diplopoda in POA and POC equals or exceeds those of the other sites (Figure 4).

The relative distribution of the macrofauna abundance between the litter and topsoil (0-5 cm) was almost equal in SEC, whereas in FLO the abundances in the soil fraction were higher (Figure 3). This is in accordance with the litter stocks, which were highest in SEC and lowest in FLO. In FLO, the relative fraction of the soil fauna in the litter layer (compared to soil) was particularly low in July and September 1997, then increased, mainly due to an increase in the abundance of predators. In POA and POC, generally more fauna was found in the soil than in the litter stratum, probably due to the low amount of litter at these sites.

Biomass data for these samples are currently prepared.

5.5.4 Earthworms. Earthworms can not be assessed from the macrofauna sampling program, which made separate sampling (formol extractions from large areas of 4 m^2)

necessary. Only 6 species have been identified in the material and the total number of species will remain below 10. The density of earthworms ranged from 0.1 to 5.5 ind./m^2, their biomass from 0.1 to 35.3 g fresh wt./m^2. Individual numbers were low in comparison with other tropical forest sites, but biomass was among the highest recorded so far from tropical sites. Average densities at all sites were not different, but biomass in FLO was six times higher than in SEC and in the plantations, and dominance spectra also differed between the sites (Table 3).

5.5.5 Termites

Due to their social organization and uneven distribution patterns, termites could not be adequately assessed from the standard macrofauna program, and additional, time-consuming field studies, to be concluded in 1999, were necessary to assess the size of their populations and their contribution to litter turnover.

Biomass and distribution. Biomass data of termites are still being processed (doctoral dissertation E. Gomes which started in April 1998). With bait stations (doctoral dissertation C. Hanne), eight genera of soil termites were collected in a primary forest site, five in the secondary forest, and only three in the plantation sites POB and POE (plantation system IV in blocks B and E, respectively; data from February to October 1998). In the experimental plantations, principally soil termite populations are more reduced than other food guilds. This shows that functional diversity may be negatively affected in the agricultural/forestry sites.

Food preference and the biology of the large and abundant, soil-inhabiting and leaf-feeding *Syntermes* are being studied in a dissertation by Lucilene Medeiros (no reports available).

Respiration. The respiration rates of termites differ according to food guild (wood-feeders> generalists>humivorous>leaf-feeders; doctoral dissertation C. Hanne) and also according to caste (soldiers and workers differ in size). The data will allow to present a differentiated picture of the impact of termite populations in our study, according to food guild and biomass.

Swarming. The mestrado study of Angelica Rebello, based on collections of swarming termite alates with light and flight traps (Rebello 1998), was initiated 1994 together with Dr. Preisinger of ENV 23. It shows that swarming termites (alates which are founders of new colonies) have a large potential to colonize the plantations. Of alates from 44 collected termite species, 14 species occurred exclusively in the mixed culture system, 12 were exclusive to rain forest, and 18 species were found in both sites. This shows that site-specific characteristics, e.g. the lack of hiding places for nest-founding couples or unfavorable microclimatic conditions, are responsible for the low population density of termites in the plantations, not the lack of swarming. This opens good prospects for the manipulation of these factors in order to enhance termite populations in the plantations.

Humic substances in termite nests. Preliminary data of a project carried out in cooperation with the University of Bayreuth show that, as lignin is selectively concentrated in the termite nests to levels above those in wood, nests become more resistant to decay, thus probably contributing to the formation of a nutrient mosaic in the soil (cf. Abstracts Amelung et al. in the Annex).

5.6 Decomposition rates and fauna in litter bags and mini-containers

5.6.1 Litter bags. The first series of litter bags has now been completely analyzed. The data show that the decomposition rate is high only in the presence of the macrofauna (large soil fauna like earthworms, termites, diplopoda, isopoda in the coarse mesh size of 1 cm). In the primary forest (FLO) site, decay rates were significantly reduced to almost 25% when macrofauna was excluded (in litter bags of mesh size 250 and 20 µm; Table 4; Figure 5). The mesofauna could not compensate for the exclusion of the macrofauna.

Litter decomposition was fastest in the coarse mesh bags of the primary forest (FLO) site (annual decay coefficient k = 2.30), followd by POC and SEC, and lowest in POA (k=0.58; Table 4).

5.6.2 Mini-containers. In the first series of mini-containers, decay rates were about 5% faster than in the litter bags, probably because the material exposed in this way (leaf discs of 0.6 mm diameter) was already more comminuted than the whole leaves exposed in litter bags. The relative differences between the decomposition rates in the different areas and mesh sizes, however, were similar in both experiments. Weight losses in the containers with medium mesh (mesofauna) were always higher than in bags with the finest mesh (microflora only) (Table 4).

The contribution of macrofauna can not be assessed with this method, a serious shortcoming in view of the eminent importance of the macrofauna shown in the litter bag trials. Nevertheless, mini-containers may allow site comparisons in studies of specific scopes.

5.6.3 Mesofauna in litter bags. Only data for the first four (of seven) sampling periods of the first litter bag series (started 27.10.97) are available. Sixty-eight per cent of the total of collected arthropods were Acari, and of these 63% were Oribatida. The density of Acari in the fine mesh was very low which shows a successful separation of mesofauna and microflora with the 20µm mesh size (the few individuals found in the fine mesh bags are thought to have ecloded from eggs that were laid through the mesh). The total number of arthropods in the bags was highest in FLO, followed by POA/POC and SEC. Enchytraeidae and Naididae abundances in litter bags were very large in FLO, lower in SEC, and almost zero in POA and POC. This is in agreement with the decomposition rates in the three sites, which follow the same order.

5.6.4 Phenolics in litter bags. Phenolic substances are feeding deterrents stored in plant tissue. Their concentrations in the *Vismia* leaf material enclosed in the litter bags decreased almost linearly to 10-40% in 168 days of decomposition and was quite uniform at 10-20% after 252 days. No influence of site and mesh size can be seen, showing that phenolics were probably released via leaching rather than by biogenic processes from the leaves.

5.7 Feeding activity of soil fauna in bait-lamina

Bait lamina are narrow plastic strips with sixteen 1-mm holes that contain cellulosic bait material, widely applied in temperate regions to determine a "soil fauna feeding activity" (not further specified). For the first time, the bait lamina test has been applied in the tropics. In order to do this, we had to reduce the standard exposition time of 19 days to four days, but no other adaptations to tropical conditions seemed necessary.

At the moment, bait lamina data are available for June and December 1997, and June and September 1998. Analysis is based on the number of "holes" fed upon and/or the frequency of bait lamina attacked at each site irrespectively of the number of holes emptied. In both cases and in all months which were analyzed, the result was the same: Percent feeding and frequency were always highest in POA/POC, and lowest in FLO. This is in sharp contrast with the data on soil fauna numbers and biomass at the sites. The result may point to a lower availability of palatable food resources at POA/POC which leads the organisms to "jump on the baits". However, the reaction of soil fauna groups to bait lamina is still not totally understood, and further behavioral and feeding studies are under way.

5.8 Carbon and Nitrogen Analysis

5.8.1 C/N in litter bags. The relative concentration of nitrogen is seen as an indicator of the degradability (higher N content pointing to better degradability). The relative concentration of nitrogen in leaves of *Vismia* (used in the litter bag experiments), is similar to Andiroba and Mogno (all have 1.2-1.4% N), only in the leaves of *Hevea* sp. (1.8%) and *Pueraria* sp. (2.2%) the N concentration is higher. For tropical conditions this decomposition rate is relatively low, which shows that *Vismia* is a rather recalcitrant litter type.

The initial N content of the *Vismia* leaf material put in the litter bags was already considerably lower (0.74%) than that of freshly fallen leaves (1.2%), showing that leaching had already occurred when we collected the leaves. During the first month of exposition in the field the relative concentration of N in the remaining litter still decreased in the polyculture areas but not in FLO and SEC. In the further course of the experiment N concentrations increased steadily in all areas. After one year in the field, nitrogen contents were always highest in the coarse mesh bags and distinctly higher in FLO and POC (1.7%) than in SEC and POA (1.3%). The significant difference of C/N ratios in the remaining litter in litter bags with and without access of macrofauna again shows the importance of the macrofauna for the decomposition subsystem (Table 5).

5.8.2 C/N in mini-containers. The data show the same trends as those of the litter bags, with the exception that, in accordance with the increased decay rate in the mini-containers, N concentrations also increased more rapidly.

6. Scientific production

6.1 Publications

Amelung, W., Martius, C., Garcia, M., Kueper, U., Ullbrich, D., Zech, W. (1998 in press): **Organic matter in termite mounds of an Amazonian rain forest**. Proceedings III Workshop SHIFT, Manaus, Brazil

Beck, L., H. Höfer, C. Martius, J. Römbke, M. Verhaagh (1997): **Bodenbiologie tropischer Regenwälder**. Geographische Rundschau 1/1997, 24-31

Beck, L., Gasparotto, L., Förster, B., Franklin, E., Garcia, M., Harada, A., Höfer, H., Luizão, F., Luizão, R., Martius, C., de Morais, J. W., Oliveira, E., Römbke, J. (1998a in press): **The role of soil fauna in litter decomposition in primary forests, secondary forests and a polyculture plantation in Amazonia (SHIFT Project ENV 52): Methodological considerations.** Proceedings III Workshop SHIFT, Manaus, Brazil

Beck, L, Höfer, H, Martius, C, Garcia, MB, Franklin, E, Römbke, R (1998b in press): **Soil fauna and litter decomposition in primary and secondary forests and polyculture system in Amazonia - study design and methodology**. Proceedings III Workshop SHIFT, Manaus, Brazil

Fagundes, E.P. & Franklin, E.N. **Ácaros do solo (Acari: Oribatida), abundância e papel na decomposição de liteira em floresta primária e numa área de policultivo de madeira da Amazônia.** Anais da VII Jornada de Iniciação Científica do Amazonas, 7-9/07/1998, Campus do INPA, Manaus, AM., Brasil. pp.32-34.

Förster, B., M. Farias, R. Luizão (1998 in press): **Microbial respiration and biomass in tropical forest soil and litter**. Proceedings III Workshop SHIFT, Manaus, Brazil

Hanne, C., Martius , C. (1998 in press): **Impact of Amazonian termite populations on the carbon cycle of differently used forest systems: CO_2 production of different termite food-guilds.** Proceedings III Workshop SHIFT, Manaus, Brazil

Höfer, H., Martius, C., Römbke, J., Garcia, M.B. , Beck, L. (1998): **SHIFT Project ENV 52: Soil Fauna and Litter Decomposition: The Use of Adapted Soil Biological Methods in Amazonian Rain Forests** In: H. Dalitz et al. (ed.): Bielefelder Ökologische Beiträge Band 12. Kurzbeiträge zur Tropenökologie DFG Abschlußsymposium "Mechanismen der Aufrechterhaltung tropischer Diversität, 18.-19.2.1998 und 11. Jahrestagung der Deutschen Gesellschaft für Tropenökologie, 20.-22.2.1998 Bielefeld, Germany, p. 111.

Martius, C. (1998): **Ressourcennutzung durch Termitenpopulationen und ihre Funktion in tropischen Ökosystemen**. In: H. Dalitz et al. (ed.): Bielefelder Ökologische Beiträge Band 12. Kurzbeiträge zur Tropenökologie DFG Abschlußsymposium "Mechanismen der Aufrechterhaltung tropischer Diversität, 18.-19.2.1998 und 11. Jahrestagung der Deutschen Gesellschaft für Tropenökologie, 20.-22.2.1998 Bielefeld, Germany, p. 41.

Martius, C., J. Römbke, M. Verhaagh, H. Höfer, L. Beck (1997 submitted): **Termiten, Regenwürmer und Ameisen - prägende Elemente der Bodenfauna**

tropischer Regenwälder. Geographische Rundschau.

Römbke, J.: **Enchytraeid "hunting" in a tropical rain forest - an example from Manaus (Amazonas, Brazil)**. Newsletter on Enchytraeidae (submitted).

Römbke, J., Höfer, H., Martius, C., Förster, B., Franklin, E., Garcia, M., Beck, L. (in press): **Die Rolle der Bodenfauna beim Streuabbau in Primär- und Sekundärwäldern und einer Holz-Mischkulturplantage in Amazonien (SHIFT Projekt ENV 52): Methodische Überlegungen**. In: Markert, B. & Oehlmann, J. (eds.): Ökosystemare Ansätze in der Ökotoxikologie. 3. Deutschsprachige SETAC Europe-Tagung. G. Fischer-Verlag, Jena.

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Römbke, J. , M. Meller & M. Garcia (1998 in press): **Earthworm densities in central Amazonian primary and secondary forests and a polyculture forestry plantation.** Proceedings III Workshop SHIFT, Manaus, Brazil

6.2 Presentations at Congresses and Workshops

Amelung, W., Martius, C., Bandeira, A.G., Garcia, M., Gonter, T., Zech, W.: **Lignin and other organic substances in termite mounds of moist and dry ecosystems in Brazil.** Jahrestagung der Gesellschaft für Ökologie, Ulm, September 1998.

Amelung, W., Martius, C., Garcia, M., Kueper, U., Ullbrich, D., Zech, W.: **Organic matter in termite mounds of an Amazonian rain forest**. III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Amelung, W., Martius, C., Garcia, M., Zech, W.: **Organische Bodensubstanz in Dichtefraktionen von Termitennestern unterschiedlicher Gattung im Regenwald Amazoniens, Brasilien.** Sitzung der Kommission Bodenbiologie der Deutschen Bodenkundlichen Gesellschaft, Dresden, Germany, November 1998.

Beck, L.: **Streuabbau und Bodenfauna in Wäldern gemäßigter und tropischer Breiten.** Jahrestagung der Gesellschaft für Ökologie, Ulm, September 1998.

Beck L., Gasparotto, L., Förster, B., Franklin, E., Garcia, M., Harada, A., Höfer, H., Luizão, F., Luizão, R., Martius, C., de Morais, J. W., Oliveira, E., Römbke, J.: **The role of the soil fauna in the litter decomposition process in primary forests, secondary forests and a polyculture plantation in Amazonia (SHIFT Project ENV 52).** III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Fagundes, E.P. & Franklin, E.N., Morais, J.W., Luizão, F.L., Martius, C. & Beck, L. 1998. **Ácaros do solo (Acari: Oribatida), abundância e papel na decomposição de liteira numa floresta primária, floresta secundária e numa área de policultivo de madeira da Amazônia.** II Congresso Sulamericano de Alternativas de Desenvolvimento - Instituto Luterano de Ensino Superior; 06 a 09/10/1998.

Fagundes, E.P. & Franklin, E.N., Morais, J.W., Luizão, F.L., Martius, C. & Beck, L. 1998. **Ácaros do solo (Acari: Oribatida), abundância e papel na decomposição de liteira numa floresta primária, floresta secundária e numa área de**

policultivo de madeira da Amazônia. XIII Semana de Biologia do Amazonas - SEMBIO, 14-18/12/1998.

Farias, M., B. Förster, R. Luizão: **Microbial respiration and biomass in tropical forest soil and litter**. III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Franklin, E., M. Garcia, F. Luizão, R. Luizão, J.W. de Morais, E. Oliveira: **SHIFT project ENV 52: Soil fauna and litter decomposition. The use of adapted soil biological methods in Amazonian rain forests: Mesofauna**. III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Garcia, M., Höfer, H., Martius, C., Römbke, J., Ott, R., Beck, L.: **SHIFT project ENV 52: Soil fauna and litter decomposition. The use of adapted soil biological methods to study macrofauna in Amazonian rain forests**. III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Hanne, C., Martius, C.: **Impact of Amazonian termite populations on the carbon cycle of natural and managed forest systems: respiration rates in different termite food guilds**. VII. International Congress of Ecology INTECOL 1998, Florence, Italy 19-25 July, 1998.

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Luizão F.J., Franklin, E., Oliveira, E.P, de Morais, J.W., Höfer H., Martius, C., Beck, L.: **Litter-bag experiments on decomposition and mesofauna colonization of leaves in primary and secondary forests on degraded croplands in central Amazonia.** III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998.

Martius, C., Höfer, H., Römbke, J., Garcia, M.B.Beck, L.: **Shift Project ENV 52: Soil fauna and litter decomposition - the use of adapted soil biological methods in amazonian rain forests**. VII International Congress of Ecology INTECOL 1998, Florence, Italy 19-25 July, 1998.

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Römbke, J., Höfer, H., Martius, C., Förster, B., Franklin, E., Garcia, M., Beck, L.: **The role of the soil fauna in the litter decomposition process in primary forests, secondary forests and a polyculture plantation in Amazonia (SHIFT Project ENV 52): Methodological considerations.** 3. Deutschsprachige SETAC Europe-Tagung.

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7. Tables

Table 1: Site microclimate. Monthly values and total average temperature (°C) and humidity (% r. h.) values for the first study interval 22.7.97 - 4.2.98 (197 days), L = litter, S = soil. POC soil data are lacking. Data from report of Martius

	Temperature								Air Humidity in the Litter Layer		
Site	FLO		SEC		POA		POC		FLO	SEC	POA
Litter/Soil	L	S	L	S	L	S	L	S	L	L	L
Logger No.	109	112	110	114	111	115	118	116	966	970	973
Mean	26.4	26.1	26.4	26.1	28.4	26.6	26.6	n.d.	96.6	90.5	86.9
S.D.	1.8	0.7	1.9	0.8	5.5	1	2.1	n.d.	8.64	15.7	20
% of FLO (L)	***100***	*98.6*	*99.9*	*98.7*	*107.6*	*100.6*	*100.6*	*n.d.*	***100***	*93.7*	*90*
Maxima	34.7	27.7	32.6	28.8	50.9	29.9	36.5	n.d.	100	100	100
Minima	22.6	23.7	22.8	23.8	22.2	23.1	22.8	n.d.	43.6	29.6	20.6

Table 2: Average temperature (°C) and humidity (% r. h.) values for the second study interval 26.5.1998 - 19.11.1998 (177 days). L = litter, S = soil. Data from report of Martius

	Temperature										Air Humidity in the Litter Layer			
Site	FLO		SEC		POA		POC		Additional Sites		FLO	SEC	POA	POC
									PupC	PolyII-B				
Litter/Soil	L	S	L	S	L	S	L	S	L	L	L	L	L	L
Logger No.	109	114	110	115	111	118	112	569	570	572	66	70	73	73
Mean	25.6	25.7	25.7	25.9	26.8	26.3	25.8	25.6	25.6	29.7	96.9	99.3	92.5	99.3
S.D.	1.3	0.5	1.2	0.4	3.2	0.9	2.4	0.6	2.5	7.3	16.1	3.2	17.4	2.7
% of FLO (L)	***100***	*100.1*	*100.2*	*101.1*	*104.4*	*102.4*	*100.6*	*99.8*	*100.0*	*116.0*	***100***	*102.5*	*95.5*	*102.5*
Maxima	30.1	27	28.9	27	46	28.9	30.1	27.1	36.2	55.7	100	100	100	100
Minima	22.9	24.5	23.2	24.9	22.9	24.3	22	23.9	21.9	22.2	0.5	72.6	0	76.1

Table 3: Number (Ind./m^2) and biomass (fresh weight, g /m^2) of earthworms from the four study plots. Data taken from report of Römbke.

	FLO		SEC		POA		POC	
Month	Ind./m^2	g /m^2	Ind./m^2	g /m^2	Ind./m^2	g /m^2	Ind./m^2	g /m^2
07/97	0.8	19.2	1.3	4.1	2	7.3	0.8	8.6
09/97	0.5	11	0.6	1.1	0	0	1	21.6
12/97	2	20.3	0.8	5.6	0.5	0.1	0.5	0.3
03/98	2.5	8	3.2	3.8	1.8	0.4	9	3.9
06/98	4.1	8	1.6	3	2	n.d.	1.2	n.d.
09/98	1.3	35.3	0.5	0.7	0	0	0.8	0.8

Table 4: Decomposition rates calculated from non-linear regressions (exponentiell decay) of remaining litter weight in litterbags (first series; data from report of Höfer). k = decay coefficient in litterbags; t_{50} = half-life time of litter weight

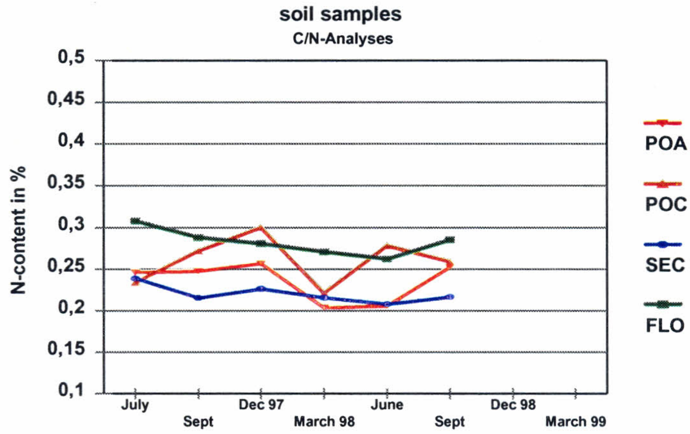
Study site	Mesh width	**Litter bags**			**Mini-container**
		k/day litterbags	**k/year**	t_{50} [days]	t_{50} [days]
FLO	1000 µm	0,0064	**2,34**	108	-
	250 µm	0,0017	**0,62**	408	321
	20 µm	0,0020	**0,73**	346	376
POA	1000 µm	0,0016	**0,58**	433	-
	250 µm	0,0011	**0,40**	630	409
	20 µm	0,0011	**0,40**	630	483
POC	1000 µm	0,0038	**1,39**	182	-
	250 µm	0,0015	**0,55**	462	407
	20 µm	0,0018	**0,66**	385	442
SEC	1000 µm	0,0024	**0,88**	289	-
	250 µm	0,0008	**0,30**	845	338
	20 µm	0,0011	**0,40**	630	386

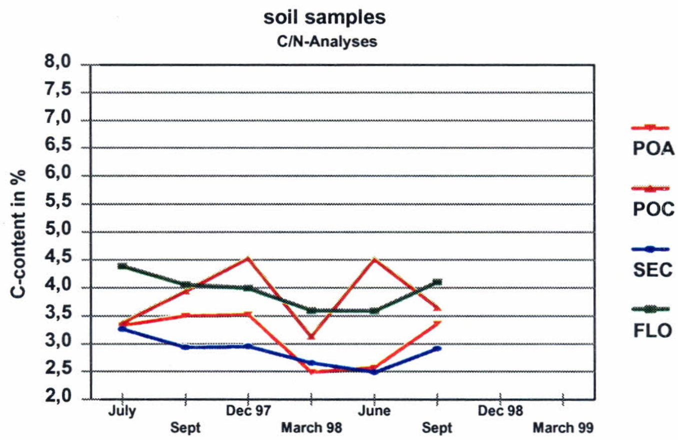
Table 5: Carbon and Nitrogen contents of *Vismia* leaf material retrieved from litter bags (first series)

		1. retrieval			2. retrieval			4. retrieval			5. retrieval			6. retrieval		
	mesh	N	C	C/N	N	C	C/N	N	C	C/N	N	C	C/N	N	C	C/N
POA	coarse	0.67	49.56	74.48	0.75	49.02	66.04	0.87	49.24	57.14	0.88	48.32	54.96	1.23	46.33	38.96
	medium	0.73	49.34	68.30	0.77	49.06	64.90	0.87	50.54	60.13	0.93	49.05	53.35	0.98	47.60	49.13
	fine	0.66	49.18	75.80	0.78	49.13	64.38	0.93	49.13	52.91	0.89	49.34	56.14	0.95	48.71	52.25
POC	coarse	0.74	49.86	67.97	0.77	48.85	63.37	1.06	48.99	46.33	1.09	48.17	44.44	1.27	46.06	36.49
	medium	0.71	49.92	71.00	0.71	49.02	69.61	0.91	49.50	54.94	0.93	49.00	52.87	1.07	48.08	45.88
	fine	0.72	49.36	69.61	0.69	49.07	71.54	0.84	49.01	58.21	0.94	48.70	52.14	1.03	48.50	47.27
SEC	coarse	0.77	49.31	64.27	0.79	49.11	62.46	0.83	49.21	60.59	0.99	48.53	49.23	1.14	47.51	42.10
	medium	0.76	49.52	65.29	0.76	49.14	65.08	0.88	50.04	58.29	0.89	48.98	55.12	1.06	49.16	47.47
	fine	0.78	49.54	63.69	0.78	49.26	63.26	0.89	50.18	58.65	0.91	49.19	53.93	1.09	49.23	46.12
FLO	coarse	0.77	49.27	63.89	0.81	48.79	60.71	1.04	48.91	47.75	1.30	47.75	38.85	1.35	46.97	34.99
	medium	0.77	49.27	63.95	0.83	48.85	60.49	0.98	49.04	51.00	1.12	49.36	44.26	1.28	48.39	38.53
	fine	0.81	49.35	61.33	0.86	49.05	57.14	1.04	49.57	48.85	1.23	49.26	40.62	1.29	48.27	3753.0

8. Figures

Figure 1: Concentrations of nitrogen and carbon, and C/N ratios in soil samples of the study sites. Data from report of Höfer.





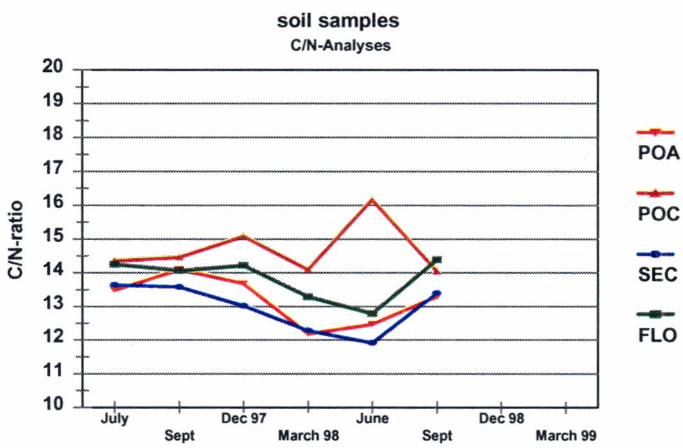


Figure 2: Litter production (above), litter stocks (middle), and calculated decay coefficient k_e for each month of the study period. From unpublished data of Martius & Garcia

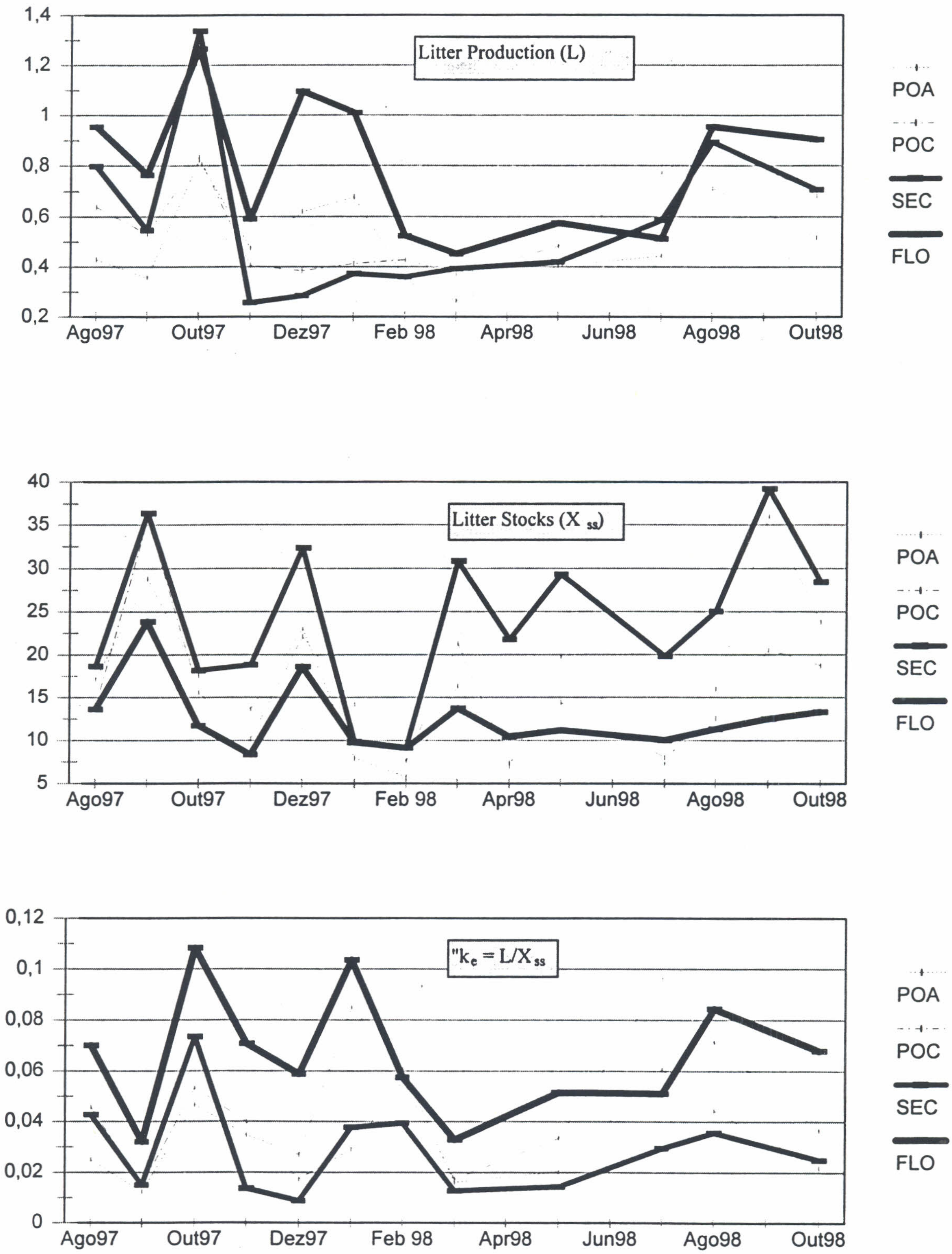
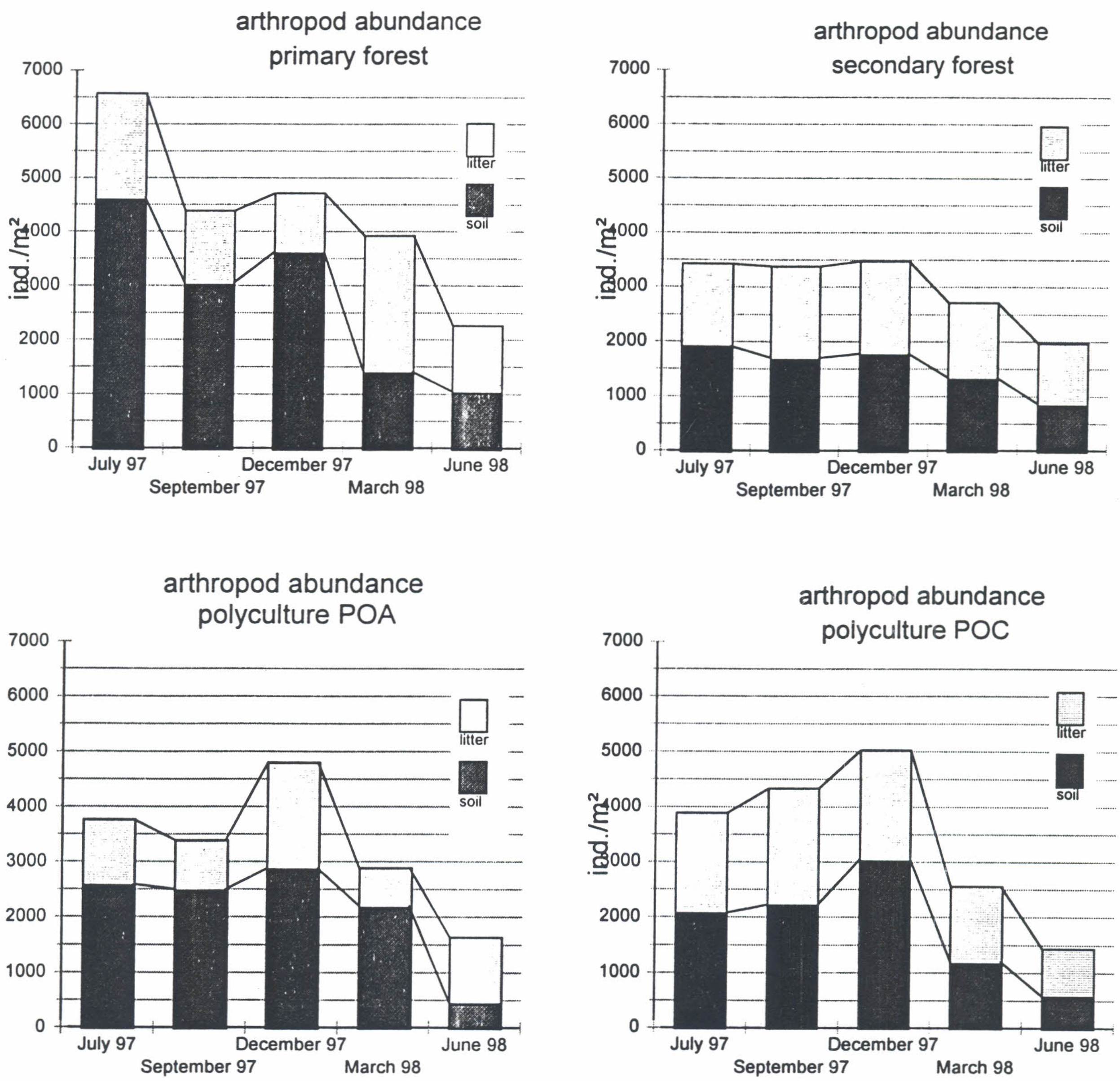


Figure 3: Macrofauna abundance from Berlese samples by layer (litter and topsoil 0-5 cm)



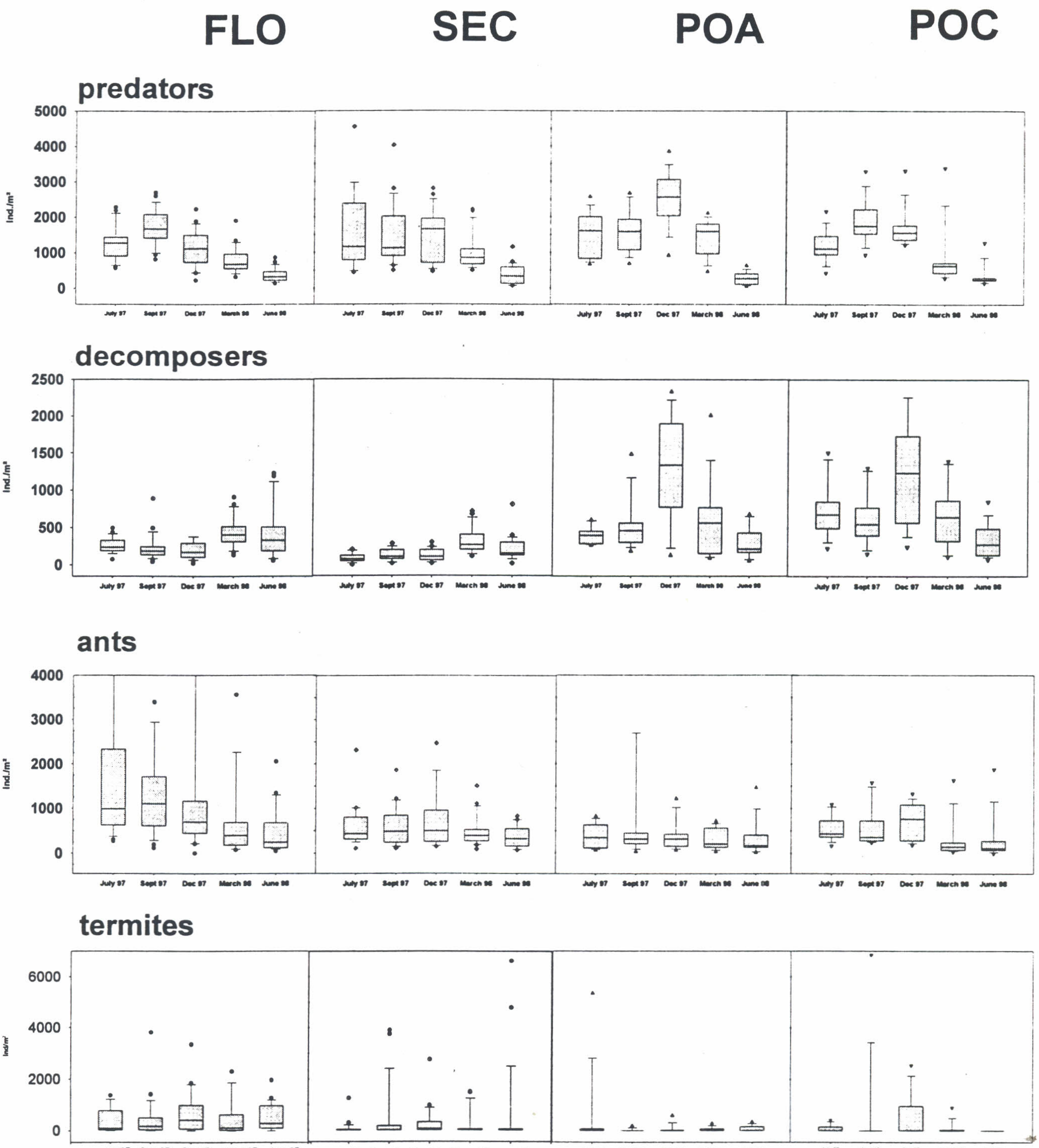
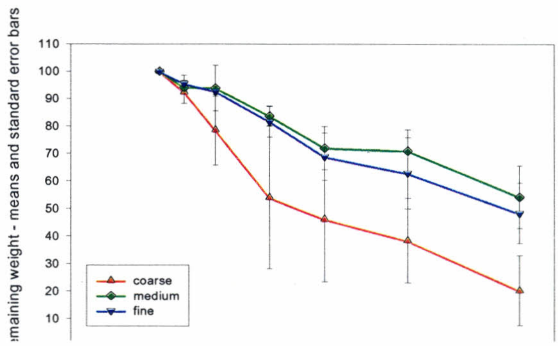


Figure 4: Data on selected macrofauna groups from the soil core sampling and extraction with the Berlese apparatus July 1997 to June 1998

Figure 5: Decomposition in litterbags (first series, exposed October 1997): Remaining leaf weight in %

FLO



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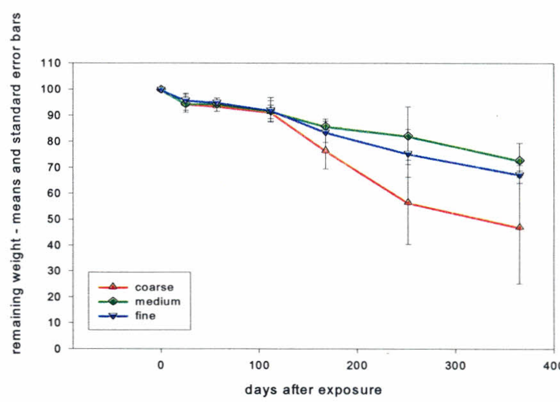

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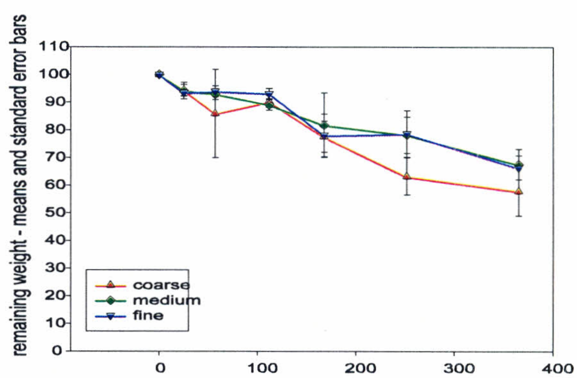
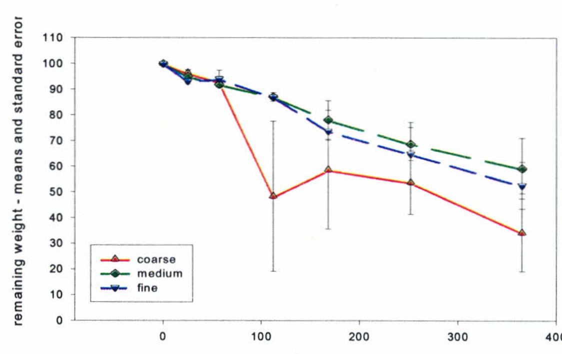


POC



9. Annex: Individual Reports

Contents