

Microclimate in agroforestry systems in central Amazonia: does canopy closure matter to soil organisms?

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Abstract

Microclimate was recorded and soil organisms were collected 1997–1999 in ecosystem stands of contrasting structure in central Amazonia (a primary forest, a 12-year secondary forest, two different agroforestry systems, a rubber tree (*Hevea brasiliensis*) plantation, and a peach palm (*Bactris gasipaes*) monoculture with a densely closed canopy). The aim was to look at the effects of canopy closure on microclimate and soil organisms. Monthly maxima temperature, average air and soil temperatures, and saturation deficit were highest in September 1997, and total annual rainfall in 1997 was 12–28% lower than in the other study years. The monthly average litter temperatures were consistently 2–4 °C higher in the plantation sites than in the rainforest and the secondary forest, and temperatures on single days (not the monthly averages) in the plantations were up to 10 °C higher than in the primary forest. The highest average litter and soil temperatures and the highest temperature maxima were recorded in the agroforestry plantations. Canopy closure strongly determined the litter temperatures in the sites. Soil macrofauna biomass was also strongly correlated to canopy closure (linear regression, $P = 0.05$). We conclude that a well developed canopy effectively protects the soil macrofauna from high temperature variation and drought stress. Therefore, optimizing these agroforestry systems for canopy closure may contribute to a better management of the beneficial soil decomposer community.

Introduction

Rainforests in the central part of Amazonia are threatened by large-scale clearings but also by the traditional slash-and-burn practice of small farmers (Lal 1995). The tropical rainforest ecosystem is known for its low resilience against disturbance; and generally, the attempts to transform it into conventional agroecosystems based on annual crops have

failed (e.g., Anderson 1990; al 1995). A potential remedy is seen in the establishment of perennial multi-species cropping systems, supposing that diversity of agricultural systems matters for productivity as it enhances the biomass and nutrient stocks (Jolliffe 1997; Naeem et al. 1996; Nijs and Roy 2000). Another option is to design cropping systems that involve trees and mimic the stand structure of the successional rainforest (Ewel 1999), thus reproducing in particular the microclimate in these stands. Microclimate is a factor that determines the environmental conditions not only directly for the crop but also for

[†] This paper is dedicated to the memory of our dear friend and colleague, Dr. Werner Hanagarth, who unexpectedly passed away on September 2, 2003

the soil organisms. It is believed that in stands managed according to these principles, soil fauna and soil microbes will encounter lower average surface temperatures and fewer extremes, a higher soil moisture and especially a lower variation of these factors, and that the beneficial soil biota that regulate nutrient cycles and physical properties of the soil (e.g., Lavelle et al. 1997; Amelung et al. 2001) can thus be maintained.

Although it is well known that most soil organisms in temperate forests (e.g., Collembola, Isopoda, Oribatei) show narrow and low temperature preferences and are highly sensitive to high temperatures, little applied knowledge is available on heat or drought stress in animals and plants in the humid tropics, or more specifically on the limiting microclimatic conditions for tropical soil fauna (Borchert 1994). Most soil organisms in rainforests require high moisture (e.g., an air humidity of 90-100%), and some can even be considered to be aquatic (Collado and Schmelz 2000). With higher temperatures, soil moisture becomes more important. Soil moisture and soil temperature seem to be quite constant in natural forest ecosystems (cf. Bohlman et al. 1995 for a Costa Rican cloud forest). In anthropogenic systems, however, which have a much simplified structure compared to the natural forest, climatic extremes are supposed to be higher and more frequent.

We investigated the microclimate in several experimental agroforestry stands in central Amazonia over a period of three years including the extreme climatic year of 1997, an El Niño (ENSO) year (Wolter and Timlin 1998). One particular interest was to look at the effects of stand structure (degree of canopy closure) on microclimate and indicators of soil life in the stands.

Here, we report on microclimate recordings from data loggers in different stands in central Amazonia together with weather station records of local climate which are used to assess the macroclimate and the inter-annual variability. We first link microclimate data to canopy closure in the stands, then data from soil biological assessments (soil fauna and microbial biomass and decomposition rates) to microclimate, and, thus, canopy closure to soil organisms.

Material and Methods

Study sites

The study area belongs to the agroforestry research station Embrapa Amazônia Ocidental, which is located close to the city of Manaus, Amazonas, Brazil (3°8'S, 59°52' W). The area is flat without elevations (altitude 44 – 50 m a.s.l.; Corrêa, pers. comm.).

The investigations took place in several sites on a 19 ha area that was cleared from primary rain forest in 1979/1980 in favor of a plantation of rubber trees (*Hevea brasiliensis* (H.B.K.) Muell. Arg.; Seringueira). This plantation was abandoned in 1981 due to a fungus infection, and secondary growth began to develop. In 1992, the rubber trees and the secondary growth were cut and burned and the area has since then been used as for experimental agroforestry research, carried out in cooperation between the Embrapa Amazônia Ocidental and the Institute of Applied Botany, University of Hamburg, Germany, with the objective to study the recultivation of abandoned monocultures with mixed cropping systems (Feldmann et al. 1995). The experiment consisted of the installation of different multi-crop systems that were thought to be economically viable in the region and, at the same time, ecologically sustainable. Monocultures served as control plots. Preisinger et al. (1994) recorded a total of approx. 1100 species of vascular plants in these plots. The area was divided into 90 experimental plots of a size of 32×8m each. Out of these, two polyculture systems were chosen for the present study. In both systems, four different tree species of commercial use had been originally planted. (For details cf. Höfer et al. 2001).

In one of the polyculture systems (sites named POA and POC, Table 1), the rubber tree (*Hevea brasiliensis* – Seringueira), a species of low quality wood (*Schizolobium amazonicum* Ducke – Paricá) and two native high quality wood species (*Swietenia macrophylla* King – Mogno, and *Carapa guianensis* Aubl. – Andiroba) had been planted in intermittent rows of rubber and Paricá spaced 4 m, and Mogno and Andiroba spaced 7 m; a 10 m distance was kept between the neighboring rows. The secondary vegetation coming up rapidly between the planted rows was not removed. It was dominated by *Vismia guianensis* (Aubl.) Choisy, a small tree whose population influenced especially the litter production in these sites. *Vismia* is a typical pioneer species in rainforest gaps (Whitmore 1998).

Table 1. Study sites at the Embrapa Amazônia Ocidental, Manaus, Amazonia, Brazil, and periods of microclimatic measurements.

Site Code	Description	Measurement Periods
FLO (Primary forest)	Primary rain forest	Aug 1997 – Mar 1998 May 1998 – Nov 1998 Nov 1998 – Apr 1999
SEC (Secondary forest)	Secondary forest established in 1984	Aug 1997 – Mar 1998 May 1998 – Nov 1998 Nov 1998 – Apr 1999
POA, POC (Wood tree culture at two sites)	Polyculture system consisting of 4 commercial species: the rubber tree (<i>Hevea brasiliensis</i>) and three wood species (<i>Schizolobium amazonicum</i> , <i>Swietenia macrophylla</i> , <i>Carapa guianensis</i>) planted in rows, between which secondary growth including trees, established in 1992, was allowed)	Aug 1997 – Mar 1998 May 1998 – Nov 1998 Nov 1998 – Apr 1999
POL (Fruit tree culture)	Polyculture culture system consisting of 4 native Amazonian fruit trees (<i>Theobroma grandiflorum</i> , <i>Bactris gasipaes</i> , <i>Bertholletia excelsa</i> , <i>Bixa orellana</i>) planted in rows, between which only annual plants, established in 1992, were admitted (the logger was placed between two rows)	May 1998 – Nov 1998
SER (Rubber stand)	Monoculture of rubber tree (<i>Hevea brasiliensis</i>), established in 1992	n/a
PUP (Palm stand)	Monoculture of peach palm (<i>Bactris gasipaes</i> ; “pupunha” in Brazil), established in 1992	May 1998 – Nov 1998

n/a= not available

The other polyculture system (site POL) consisted of four fruit tree species, *Theobroma grandiflorum* (Willd. ex Spreng.) Schum. (Cupuaçu, a popular fruit in Amazonia), *Bactris gasipaes* H.B.K. (Peach palm), *Bertholletia excelsa* H.B.K. (Brazil nut) and *Bixa orellana* L. (Orleans tree, a bush that is cultivated to produce food colorants). In this system no high-growing secondary vegetation was admitted but *Pueraria phaseoloides* (Roxb.) Benth. (Kudzu) was planted and a low grass cover had developed between the rows.

A peach palm (*B. gasipaes*) monoculture (site PUP) with 7 m high palms and a rubber tree (*H. brasiliensis*) monoculture plantation (SER) were chosen for comparison with the polyculture sites.

A largely undisturbed primary rain forest site (FLO) and a secondary forest site (SEC) near to this experimental site were also studied. The rain forest site conforms to the descriptions given by Ribeiro et al. (1999) for a nearby forest reserve. The studied secondary forest area was growing since 1984 on a former abandoned rubber plantation; during the study period it was dominated by *Vismia guianensis*, *Miconia* and *Bellucia* spp. (Preisinger et al. 1994). In both stands, sample areas of 40×40 m each were established.

The soil in the region is a Xanthic Ferralsol according to the FAO/UNESCO (1990) classification, known in Brazil as ‘latossolo amarelo’. Differences in

grain size, pH, organic matter and total N between the study plots were not significant. Only the water holding capacity was higher in the primary forest soil (FLO) than in the other plots (Martius et al. 2004).

Climate and microclimate measurements

Monthly average climate data were computed from daily recordings (January 1996 to April 1998) obtained from the standard climate station run by the Embrapa Amazônia Ocidental. Rainfall data (January 1987 to December 2000) were used for comparison. The saturation deficit was calculated from air temperature and relative air humidity according to the “Magnus formula” (Lechner 1992).

Temperature and air humidity were recorded with small data loggers (“Stowaway XTI Internal/External Temperature Logger”, range – 39 to 122 °C; “Stowaway RH Relative Humidity Logger”; Onset Computer Corporation, Porasset/MA, USA). We recorded soil temperature at a depth of 5 cm, litter temperature in the litter layer, and air humidity a few centimeters above the litter layer. Data were recorded at 10 minute intervals and stored as two-hour average values; i.e., 12 data points were obtained per day. Before being used in the field, all loggers were calibrated, and checked after two years of use, when differences between the loggers were found not to exceed 0.5 °C (see Table 1 for details).

Canopy closure

Canopy closure was recorded with a digital camera (Sony DSC-P5) mounted on a tripod, calibrated with a water level to point exactly upwards, and adjusted to wide angle. 10 shots were taken at random points in each site. We then transformed the original color picture into a graph containing only black and white pixels using standard commercial graphics software (Paintshop Pro 7). Canopy closure is the percentage of black pixels in the picture. The differences in canopy cover between the sites were assessed with an ANOVA on ranks, followed by a Tukey test for pairwise comparison (Sigmastat 2.03). Linear regressions were used to determine the relationships between canopy closure and climatic as well as pedobiological parameters.

Despite long-lasting controversies over how to best measure canopy closure (cf. Ganey and Block 1994; Cook et al. 1995; Bunnell and Vales 1990; Nakamura pers. comm. 2001), we think that, given our main interest in the canopy as an isolating layer between atmosphere and soil, the chosen approach appropriately captures the cover rate of the stands.

Soil respiration

Soil respiration was measured using the release of CO₂ from soil samples in a 17-chamber Infrared-Gas-Absorption-Spectrometer (IRGA). Soil samples 0-10 cm were taken in the field, transported to the lab, sieved through a 4 mm sieve to remove roots and large animals, and measured for 24 h. For details cf. Kurzatkowski et al. (2004).

Soil fauna

Soil fauna density and biomass in the study plots were assessed from soil and litter samples with different methods. At every sampling event (every three months, 8 times, between July 1997 and March 1998) soil samples were taken from randomized points at the polyculture plantations POA and POC (n=10/site) and at the secondary and primary forest areas (n=20/site). Mesofauna was determined from soil cores (6 cm diameter) separated into litter layer and topsoil 0-5 cm, and extracted in a Kempson apparatus (Adis 1987). Macrofauna (including termites and Isopoda) was sampled with soil cores of 21 cm diameter extracted in a Berlese-type extractor. Earthworms were extracted from soil by repeatedly pouring a 0.5% for-

mol solution to areas of 4 m² (n=1 or 2 per date) and manually collecting the emerging earthworms (cf. Römbke et al. 1999). For details cf. Höfer et al. (2001).

Litter decomposition

Litter decomposition was determined by enclosing 7-10 g of air-dried *Vismia* leaves in litterbags made of nylon mesh (width 10 mm). This mesh width allows the whole decomposer community to participate in the decomposition of the leaf material (Höfer et al. 2001). The bags were retrieved after repeated intervals, and the weight loss assessed. The annual decomposition rate was computed from a negative exponential regression fitted to the data using the software Sigmaplot.

Results

Climate (weather station)

Average annual rainfall at Embrapa between 1971 and 2000 was 2554 ± 273 mm (Figure 1). The statistically significant difference (P=0.002) between average annual rainfall in the first half of this period (1971-1985: 2408 ± 188 mm) and the second half (1986-2000: 2700 ± 270 mm) suggests that rainfall increased during the later years. The six years of the data set 1971-2000 in which the annual rainfall exceeded the average + 1 S.D. all were in the second half after 1986. Nearby, in the city of Manaus, average annual rainfall was also lower (2234 ± 219 mm) in the period 1971-1985, and higher (2392 ± 344 mm) during 1986-2000 (Hanagarth unpubl.).

In the period in question here (1996-98 for which microclimate data are available, see below), the year 1997 was one of the few extremely dry years in which annual rainfall was below the average - 1 S.D. Normally in this region, not more than 1-2 months per year have a rainfall below 100 mm (Ribeiro and Adis 1984), but in 1997, during four months rainfall remained below this threshold (Figure 2). The year 1997 was also a very hot year: the highest monthly maxima (T_{max} in Figure 3, top) and the highest average monthly air (T_{med}) and soil (T_{soil}) temperatures in the period 1996-1998 were all recorded in September and October 1997. The minimum air temperatures (T_{min}) still were elevated in the subsequent period, from October 1997 to May 1998. Both rain-

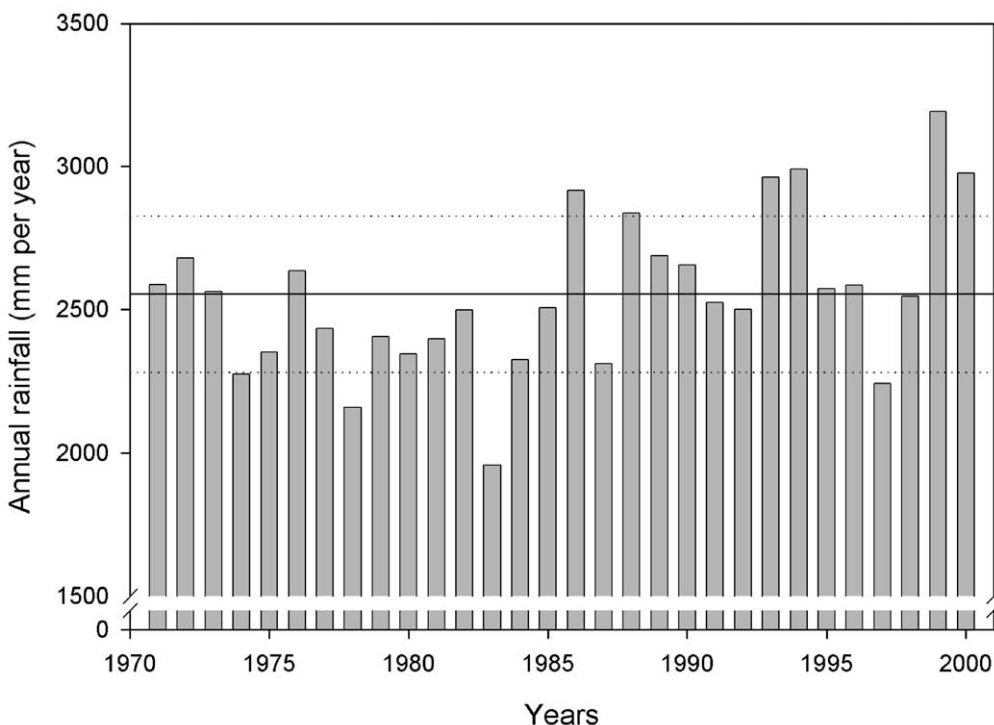


Figure 1. Annual rainfall 1971-2000 at the weather station of Embrapa Amazônia Ocidental, Manaus, Amazonia (data courtesy of Embrapa). Note the interrupted y-axis. Straight horizontal line: average rainfall (1971-2000); dotted lines: ± 1 St.Dev.

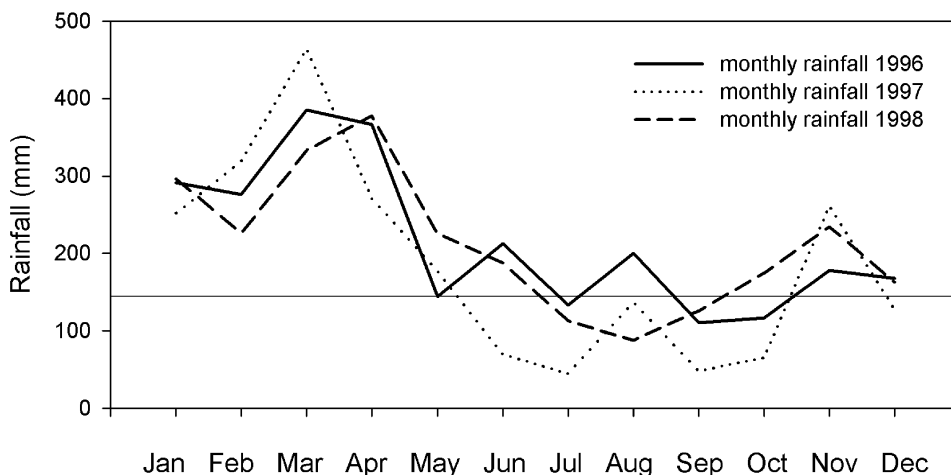


Figure 2. Monthly rainfall 1996-1999 (y-axis: monthly sums) at the weather station of Embrapa Amazonia Ocidental, Manaus, Amazônia.

fall and the number of rainy days were markedly reduced in this period (Figure 3, middle). The relative air humidity was extremely low, whereas the evapotranspiration (Piche evaporation) peaked in September 1997, and the saturation deficit was extremely high in this month (Figure 3, bottom). The year 1997

was marked by an El Niño (ENSO) event (Wolter and Timlin 1998).

Microclimate at the sites (data loggers)

The average monthly litter temperatures as recorded with loggers in the litter layer of FLO and POA re-

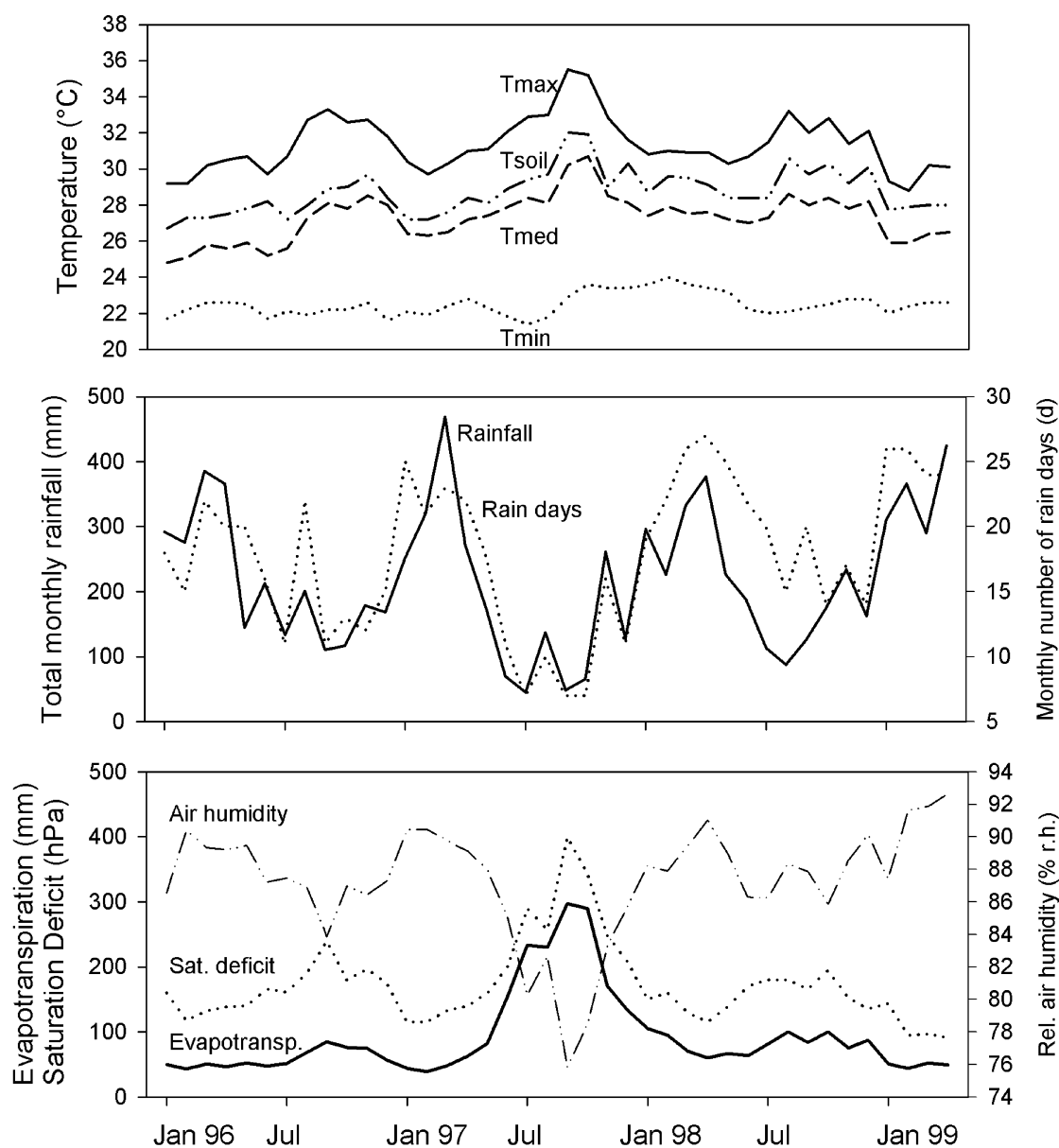


Figure 3. Climate data recorded 1996-1999 at the weather station of Embrapa Amazonia Ocidental, Manaus, Amazônia (monthly values are based on daily readings at the station; data courtesy of Embrapa): (top) average monthly air and soil temperatures; (middle) total monthly rainfall and number of rain days per month; (bottom) air humidity, average monthly evapotranspiration and calculated total monthly saturation deficit.

mained below the air temperatures recorded at the Embrapa climate station (circles in Figure 4, top), whereas the litter temperatures in the plantation POL were much higher than at the climate station (Figure 4, top). The litter temperatures differed very little when the forests (FLO, SEC), one polyculture (POC), and the peach palm monoculture (PUP) are compared,

but they were consistently higher in the plantations POA (on average about 2 °C above FLO) and POL (almost 4 °C) (Table 2; Figure 4, top). The differences are caused by the higher maxima recorded in POA and POL; the recorded minima represent the night-time temperature values and did not differ. Extreme maxima of up to 55.7 °C in POA and POL (Table 2)

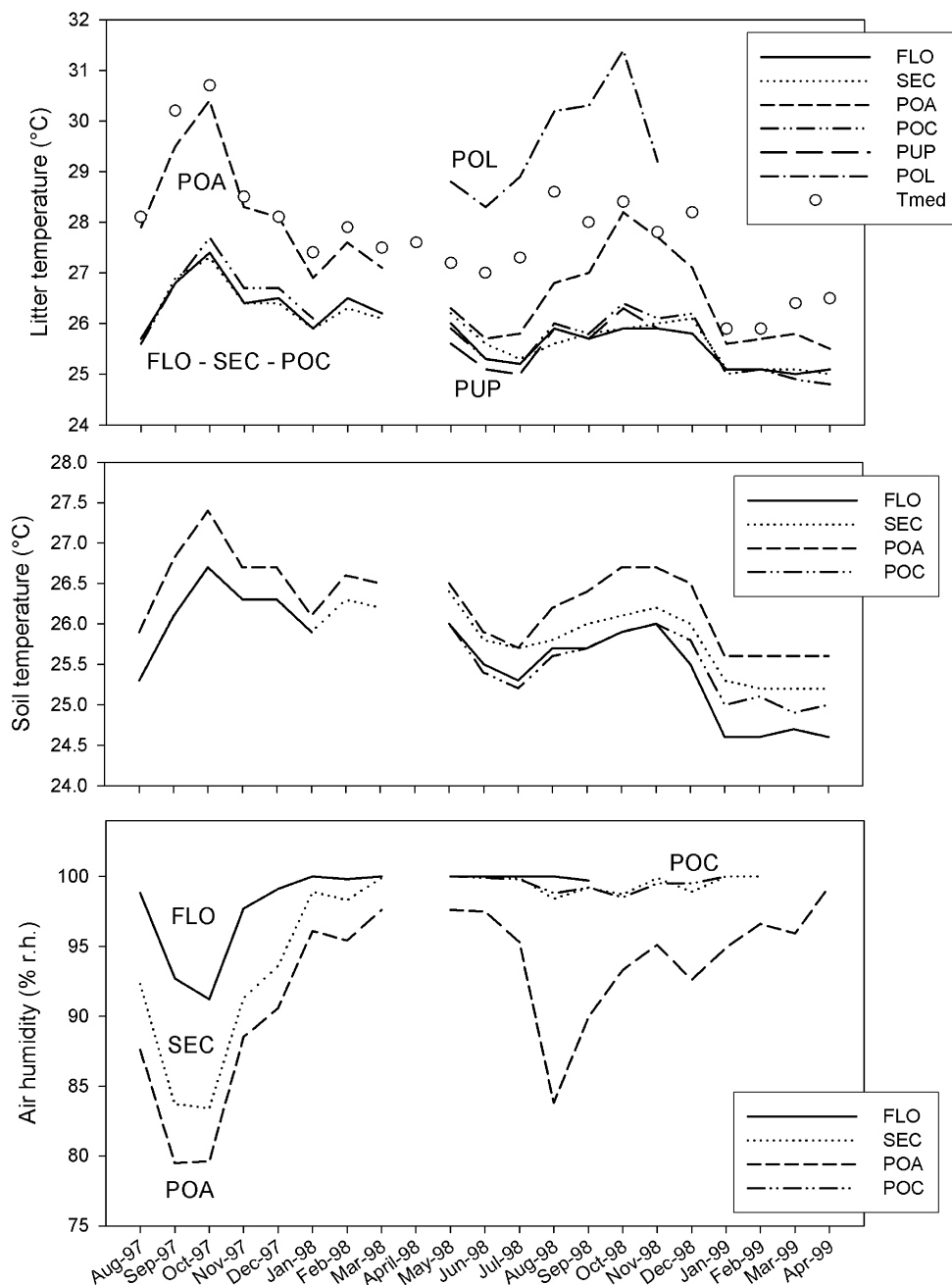


Figure 4. Monthly average microclimate values 1997-1999: (top) litter temperatures; (middle) soil temperatures; (bottom) air humidity in the litter layer; in the primary forest (FLO), secondary forest (SEC), Wood tree cultures at two sites (POA, POC), in the Fruit tree culture (POL) and in the Palm stand (PUP). Tmed= mean temperature. Embrapa Amazônia Ocidental, Manaus, Amazonia.

were probably recorded when the loggers, enclosed in translucent plastic cases, became exposed to direct sunlight, and may not represent the true temperature in the litter layer outside the case at these moments; however, these observations confirm that in these two

sites sunlight radiation reached the litter and soil surface more often than under a closed canopy. In other words, the average microclimatic conditions in the litter of the sites POA and POL were not only harsher (average temperatures higher by 2-4 °C, and humid-

Table 2. Litter and soil temperatures and relative air humidity in the study sites, Embrapa Amazônia Ocidental, Manaus, Amazonia.

	Soil temperature (°C)				Litter temperature (°C)				Relative air humidity (%r.h.)					
	FLO	SEC	POA	POC	FLO	SEC	POA	POC	FLO	SEC	POA	POC		
1997-98														
Average	26.1	26.1	26.6		26.4	26.4	28.4	26.6			96.6	90.5	86.9	
Std.Dev.	0.7	0.8	1.0		1.8	1.9	5.5	2.1			8.6	15.7	20.0	
Maximum	27.7	32.6	29.9		34.7	32.6	50.9	36.5			100.0	32.6	100.0	
Minimum	23.7	22.8	23.1		22.6	22.8	22.2	22.8			43.6	22.8	20.6	
1998-98														
Average	25.7	25.9	26.3	25.6	25.6	25.7	26.8	25.8	25.6	29.7	96.9	99.3	92.5	99.3
Std.Dev.	0.5	0.4	0.9	0.6	1.3	1.2	3.2	2.4	2.5	7.3	16.1	3.2	17.4	2.7
Maximum	27.0	27.0	28.9	27.1	30.1	28.9	46.0	30.1	36.2	55.7	100.0	100.0	100.0	100.0
Minimum	24.5	24.9	24.3	23.9	22.9	23.2	22.9	22.0	21.9	22.2	n/a	72.6	n/a	76.1
1998-99														
Average	24.9	25.4	25.9	25.2	25.2	25.3	26.0	25.3						
Std.Dev.	1.1	0.6	0.7	0.7	0.6	1.2	2.9	2.0						
Maximum	28.5	27.4	28.2	27.8	27.2	30.4	39.0	35.6						
Minimum	22.7	24.1	24.3	23.5	24.0	23.2	22.2	22.3						

Averages, standard deviations, absolute maximum and minimum values recorded in each of the three study periods (see Table 1). Due to technical reasons (logger battery life duration), the data are separated in three subsets. n/a = not available; Std. Dev. = standard deviation. Site codes: FLO: Primary forest, SEC: Secondary forest; POA/POC: Wood tree culture in two different sites; POL: Fruit tree culture; SER: Rubber stand; PUP: Palm stand.

ity lower by 5-10 percent points), they were also much more variable and unpredictable than in the other sites.

The lowest soil temperatures were recorded in the primary forest FLO, in the secondary forest SEC, and in one plantation site (POA) (Table 2; Figure 4, middle). In FLO, the soil temperatures almost equaled the temperatures in the litter layer, whereas in POA, the soil temperatures were considerably lower than the litter temperatures (Table 2). As the soil parameters were similar in all sites (Martius et al. 2004) they cannot have influenced the soil microclimate. Also, no correlation of average soil temperature and litter stocks (as indicator of the thickness of an eventually insulating litter layer) was found. Like for litter temperature, the differences in soil temperature between the sites indicate that the soil organisms face much harsher conditions in open-structured sites like POA (and, by deduction, probably also in POL) than in closed stands like FLO (Figure 4). Even small average temperature differences of, for example, 0.6 °C between FLO and POA (Table 2) will sum up to considerably large differences in temperature-days, a determining parameter for insect growth and development (Begon et al. 1996).

The monthly average air humidity at all sites was lowest in September/October 1997. In the other months, average humidity was almost always about 100% in the primary forest (FLO), the secondary forest (SEC), and one plantation site (POC), but much

lower in POA (Table 2; Figure 4, bottom). This again confirms the extreme conditions of 1997, and at the same time points to the much drier conditions in the plantation site POA, in contrast to the other three sites.

The data set that shows the original data measured in 2-hr intervals (from which the monthly averages were compiled) of the primary forest FLO, the secondary forest SEC, and the plantation site POA shows that the differences in microclimate between the sites are even more marked than the monthly averages suggest (Figure 5). Whereas air temperature fluctuates little around soil temperature in FLO and SEC, the daytime temperature peaks in the litter layer of POA are much higher. The air humidity in FLO deviates from 100% only very little, and does this mainly in the extreme year 1997 (left half of Figure 5), but not so during the first months of 1998 (right part of the Figure). In contrast, the amount and frequency of these deviations from 100% is higher in SEC, and much higher in POA. A closer look at a short interval of this data set (Figure 6) reveals that although daytime litter temperatures in FLO and SEC almost did not differ, they raised more than 10 °C above the FLO/SEC values during daytime in POA. On clouded days (e.g., the 9th and 10th peaks in Figure 6), the temperature difference still was about 5 °C. Even on rainy days the differences was still in the range suggested above by the average values, about 2 °C.

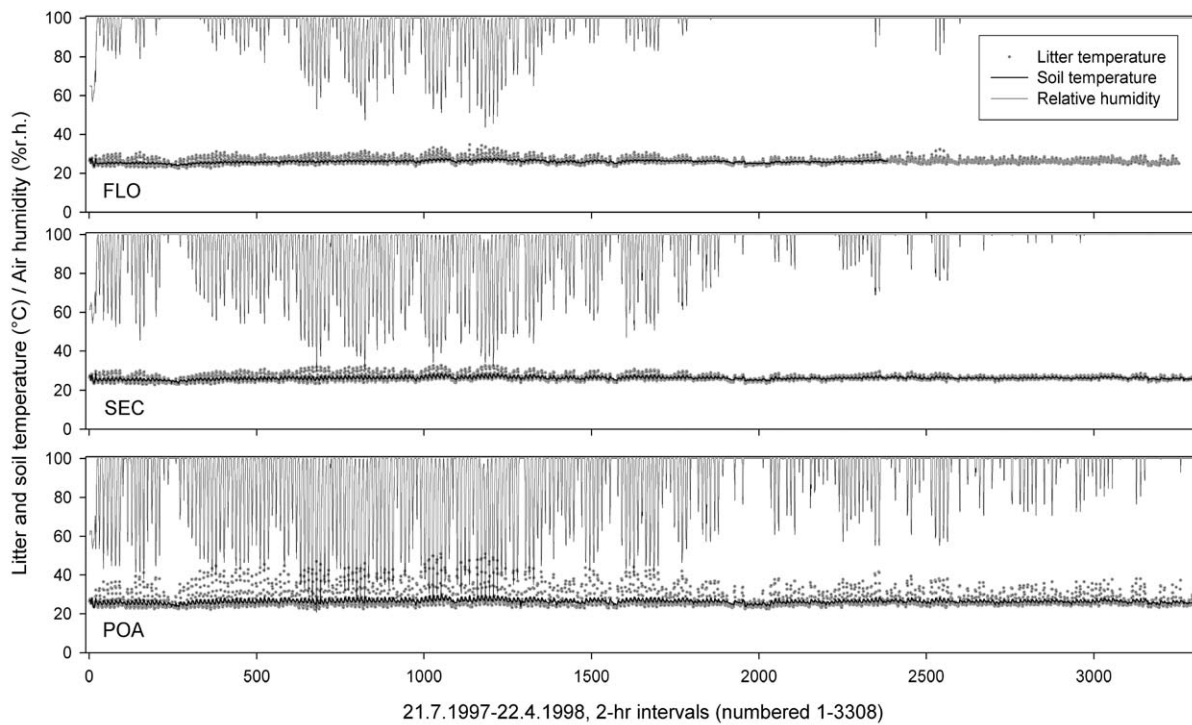


Figure 5. Microclimate data: temperature in litter (grey dots) and soil layer (thick black lines; air humidity in the litter layer (fine black line on top of each graph) in primary forest (FLO, top); secondary forest (SEC, middle), and Wood tree culture (POA, bottom). 2-hr intervals; during nine months 1997 and 1998, at Embrapa Amazonia Ocidental, Manaus, Amazônia.

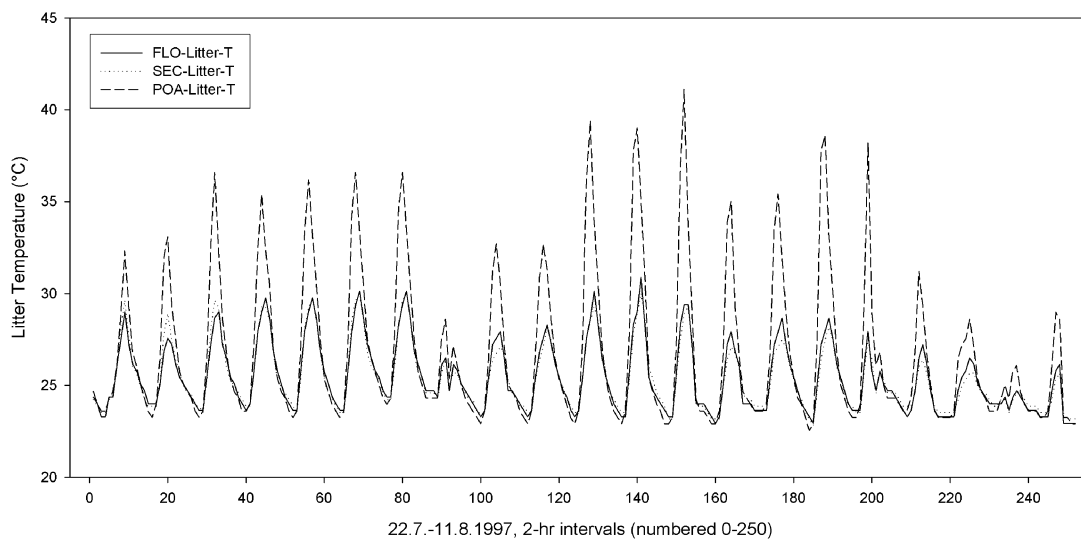


Figure 6. Daily litter temperature oscillation (Litter-T) in primary forest (FLO), secondary forest (SEC), and Wood tree culture (POA) (2-hr intervals) during three weeks in 1997, at Embrapa Amazonia Ocidental, Manaus, Amazônia.

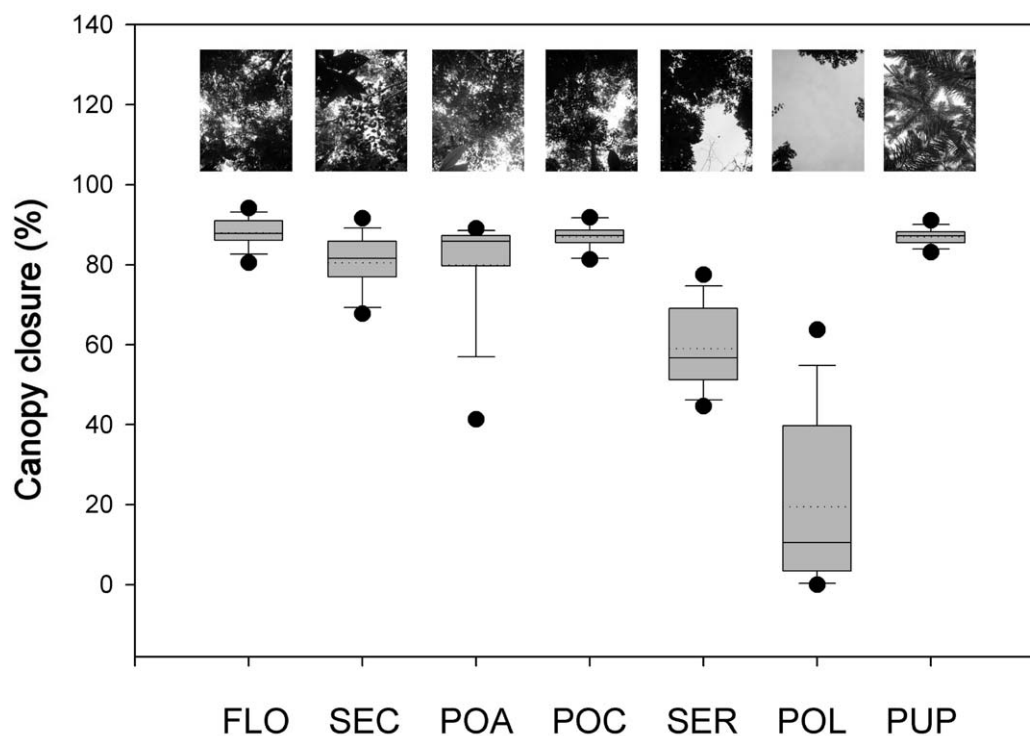


Figure 7. Average canopy closure (% black pixels) in all sites at Embrapa Amazonia Ocidental, Manaus, Amazônia. Box plots are for 10 samples per site. Dotted lines are averages, straight lines within box are medians. Box limits are 25/75% percentiles; whiskers are 10/90% percentiles, and circles 5/95% percentiles. In the top row an example of one typical canopy closure photograph is given for each site: (FLO) primary forest, (SEC) secondary forest, (POA, POC) wood tree culture at two sites, (SER) rubber stand, (POL) fruit tree culture and (PUP) palm stand.

Canopy closure

The highest canopy closure (88%) was recorded in the primary rain forest (FLO). Most of the other sites also had a rather high closure of above 80%, and principally in the polyculture area POC and in the secondary forest (SEC) canopy cover was only one percent point below that in the primary forest. However, variability of canopy cover is much higher in SEC and POA than in FLO, POC and PUP. Only the rubber tree plantation (SER; 53%) and the polyculture POL (19%) had a significantly lower canopy closure than the other sites (and also differed significantly from each other; $p < 0.005$; Figure 7 and Table 3).

The soil and litter temperatures were both highly correlated with canopy closure, although the power of the test was satisfactory only for litter temperature (Table 4). Based on this regression, canopy closure can therefore be assumed to be a good proxy of the temperature in the litter layer.

Table 3. P-values of the ANOVA on ranks, followed by Tukey test, for the comparison of canopy closure data between the study sites, Embrapa Amazônia Ocidental, Manaus, Amazonia.

	SEC	POA	POC	SER	POL	PUP
FLO	no test	0.697	no test	< 0.001	< 0.001	no test
SEC		no test	no test	0.002	< 0.001	no test
POA			no test	0.003	< 0.001	no test
POC				< 0.001	< 0.001	no test
SER					< 0.001	< 0.001
POL						< 0.001

The software does not allow to test if the difference between two values is smaller than the difference between two other values for which no difference was found. For explanation of site codes see Table 1.

Soil biology

The soil biological data followed different trends (Table 4). Soil microbial biomass was highest in POA and lowest in the rubber tree plantation and in POL (Kurzatkowski et al. 2004). Mesofauna biomass (Höfer et al. 2001) peaked only in POA, but termite

Table 4. Microbial biomass, biomass of different soil fauna groups, and decomposition rate from litter bag experiments in the study sites, Embrapa Amazônia Ocidental, Manaus, Amazonia.

Site	Microbial biomass in 0-5 cm soil					Biomass			Decomposition rate	
	$\mu\text{g C}_{\text{mic}} \text{g}^{-1} \text{ soil}$	Meso-fauna mg m^{-2}	Macrofauna ^{#)} mg m^{-2}	Four dominant macrofauna taxa ^{##)} mg m^{-2}	Meso- + macrofauna mg m^{-2}	Earthworms mg m^{-2}	Termites mg m^{-2}	k yr^{-1}		
Primary forest FLO	397	609	2713	2702	3322	1541	654	2.72		
Secondary forest SEC	423	679	1391	705	2070	259	305	0.99		
Wood tree plantation POA	460	937	1368	980	2305	397	109	0.78		
Wood tree plantation POC	409	655	2332	2537	2987	963	304	1.23		
Rubber tree culture SER	291							3.40		
Fruit tree culture POL	282							1.95		
Palm stand PUP	376							3.13		

^{#)}Without earthworms; ^{##)}Earthworms, termites, diplopods and isopods.

and earthworm biomass (Martius unpublished, Römcke et al. 2001) peaked in FLO, and macrofauna, meso- and macrofauna biomass combined as well as the four dominant macrofauna groups pooled (earthworms, termites, Diplopoda and Isopoda; Höfer et al. 2001) had their peaks both in FLO and in POC. The highest decomposition rates (Kurzatkowski et al. 2004) were measured in SER and PUP, the two monoculture plantations.

We established the regressions between canopy and different soil biological data: microbial biomass, mesofauna, macrofauna, meso- and macrofauna together, and the joint biomass of the four dominant macrofauna taxa. The best correlation coefficients were obtained for macrofauna, the 4-macrofauna-taxa group, and for meso- and macrofauna together (Table 5), although the power of the tests were generally low (in macrofauna, it was near the conventionally desired power of 0.800). Soil microbial biomass and earthworms also yielded high R coefficients but low power. The decomposition rate as determined from the litterbag experiments, a parameter that we expect to integrate soil organismic activity, failed to yield a satisfactory regression. This might be due to the fact that only one litter type was used in the litterbag experiment (Höfer et al. unpubl.), and that these tests therefore are not representative of the whole soil decomposer community in the stands. Also, only a few data points are available for these regressions, and the data should not be over-interpreted, but we conclude that canopy closure as a proxy of litter temperature has the potential to be a good predictor for the biomass of the group of the four most dominant macrofauna taxa.

Discussion and Conclusion

A closed stand canopy as in the primary rain forest site has a strong influence on microclimate in the stands and soil fauna biomass (Table 5). The canopy is able to buffer extreme climatic conditions (Figure 5; 4, top). In contrast, sites with an open canopy like the multi-tree plantation sites (POA, POL) and the rubber tree monoculture (SER) suffer from direct solar irradiation, higher litter and soil temperatures, lower air humidity in the litter, and lower soil fauna biomass. Therefore, mimicking the rain forests' canopy closure in agroecosystems would provide an efficient protection against inter-annual climatic variation as well as against microclimatic extremes. Un-

Table 5. Linear regressions ($y = ax + b$) fitted to microclimate and soil biological data as variables (y) dependent on canopy closure (x; units = canopy closure in %), for the study sites at Embrapa Amazônia Ocidental, Manaus, Amazonia.

Dependent variable y	Units of y	Regression		Correl. coeff.		Std. error estimate	Power
		a	b	R	R ²		
Soil temperature	°C	0.1	31.1	0.852	0.725	0.2	0.243
Litter temperature	°C	0.1	30.9	0.976	0.953	0.4	0.968
Microbial biomass	($\mu\text{g C}_{\text{mic}} \text{g}^{-1} \text{soil}^{-1}$)	2.1	226.0	0.818	0.67	42.1	0.634
Air humid.	% r.h.	0.3	70.7	0.414	0.172	3.6	0.064
Decompos. rate	k yr^{-1}	0.01	2.5	0.151	0.023	1.2	0.049
Mesofauna biomass	mg m^{-2}	25.7	2872.1	0.738	0.544	122.0	0.155
Macrofauna biomass	mg m^{-2}	158.3	-11319.1	0.990	0.980	117.4	0.753
Biomass of 4 dominant macrofauna groups ^{#)}	mg m^{-2}	240.4	-18423.0	0.986	0.972	213.6	0.694
Meso- and macrofauna biomass	mg m^{-2}	132.6	-8447.0	0.965	0.931	187.0	0.522
Earthworms	mg m^{-2}	129.6	-10074.3	0.938	0.879	249.3	0.405
Termites	mg m^{-2}	41.1	-3105.2	0.769	0.591	177.7	0.173

^{#)} Earthworms, termites, diplopods and isopods

der lower canopy closure (SER and POL; Figure 7) the temperature extremes became much more frequent, and daytime air humidity also decreased, often markedly (Figure 4; Figure 5 bottom).

An interesting detail is the difference between POA and POC, the two plantation sites that have the same plant composition and stand structure. Microclimate at POC, however, in general is much more similar to FLO and SEC than to POA. We assume that POC is much better protected from temperature extremes by its close neighborhood to a primary forest stand (which provides shadow to POC in the afternoon). This gives a hint that a mosaic-like landscape design in which plantations are interspersed with rainforest patches can offer additional improvement in plantation stand microclimate than would be the case on large-scale clear-cuttings (although a fragmentation of the rainforest ecosystem into too small remnants has detrimental effects on microclimate in these patches; Bierregaard et al. 2001).

The plantations differed not only in canopy closure but also in the diversity of the planted crop trees. The rubber tree and peach palm plantations (SER, PUP) were monocultures, whereas in the polyculture systems POA, POC and POL at least four tree species were planted together. The diversity of secondary growth in these stands is not considered here, but in POA and POC, the upcoming vegetation that was tolerated between the planted rows of trees added to the tree diversity of these two sites. Nevertheless, the canopy closure in these stands was not correlated to the tree diversity. SER and PUP were both monocultures, but differed completely with regard to canopy cover (Figure 7). Also, canopy cover in POA and

POC was much higher than in POL (the site with the lowest cover), although in all systems four different tree crops were planted. Although a careful choice of the structurally different trees in plantations may contribute to canopy closure, diversity alone does not have any strong influence on the microclimate within the stands. Although the admitted secondary vegetation in POA and POC buffers the soil against climatic extremes when compared to POL, this effect seems not to be related to the diversity of the secondary growth but to the increased canopy closure in these stands. The fact that microclimatic conditions in the peach palm monoculture are similar to those in the primary forest further underlines the prevalence of site structure over site diversity as a decisive factor of microclimatic conditions in the stand.

Additional data show that both the mesofauna (Mites and Collembola; Franklin et al. 2001) and the macrofauna (Höfer et al. 2001, Hanagarth et al. 2002) were relatively more abundant in the soil fraction of the samples in July and September 1997, i.e., during a period of unfavorable microclimatic conditions in the litter. They were relatively more abundant in the litter fraction during the rest of the study period (March 1998 to March 1999). This effect is strongest in the polyculture stands. We assume (although this was not measured) that the soil fauna reacts with short-term vertical migrations to changes in the moisture and temperature conditions of the litter. The differences in soil fauna densities between the studied systems averaged over the whole study period are paralleled by differences in decomposition rates (Höfer et al. 2001). The same is true for the enchytraeids and other microdrilid worms in FLO and

SEC that occurred preferentially in the litter layer at all sampling dates except in 1997 (Römbke et al. 1999), but not in POA and POC where the worms retreated to deeper layers also in the dry season of 1998 (i.e., June and September 1998). Over the whole study period, the ratio of litter fauna to soil fauna was 50:50 in FLO and SEC but 30:70 in POA and POC. (During dry periods in El Niño years, relatively more macrofauna was found in the soil, but this was not so expressed in the rainy season; POA again was the most extreme site with regard to this ratio; Hanagarth et al. 2002). Litter quantity and quality do not correlate with these results (Martius et al. 2004), and we therefore assume that it is the microclimate in the litter layer, and ultimately, canopy closure, that are most decisive for the density and distribution of the soil fauna. The microclimate in the litter and soil layers of polyculture sites is much more extreme than in secondary and primary forests in Amazonia, but a well developed canopy as in the peach palm monoculture (PUP), in the 12-year old secondary forest (SEC) or in the vicinity to a closed forest (as in POC) are factors that offer protection from high variation and high temperature peaks. These results indicate that the mimicking of a natural forest structure (closed canopy; mosaic landscape of intermittent ecosystem types instead of large-scale clear-cutting) can be successfully used for the management of microclimatic conditions that affect the decomposer fauna and microflora of the soil together with the important functions these organisms exert in the ecosystem.

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