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Density and biomass of Acari and Collembola in primary forest, secondary regrowth and polycultures in central Amazonia

Abstract

The mesofauna communities were assessed every three months (June 1997 to March 1999), in the litter and soil of a polyculture system (POA and POC) and from a primary (FLO) and a secondary (SEC) forest. The highest densities were obtained in POA, due to the dominance of Oribatida. The densities of Acari Oribatida and Collembola were notably lower in the mineral soil. For non-Oribatid Acari, the same tendency was not clearly detected. In contrary to the other groups, the highest densities of Collembola were found in FLO. In general, densities in the litter layer were higher. Therefore, strong differences were detected between 1997, an exceptionally dry year caused by the "El Niño" Southern Oscillation, and 1998. The mesofauna population was lowest in 1997 Only in 1997, was the density in FLO, POA and POC higher in the soil fraction. The pattern in SEC was not the same because of the higher amount of litter. We hypothesized that the differences between 1997 and 1998 were a result of: 1) a reaction of the mesofauna that migrated to the mineral soil during the extremely dry period of 1997 and 2) a consequence of the litter layer reduction that occurred in 1997, causing lower mesofauna densities. Superimposed on the micro-climatic factors, we observed the influence of the condition of the litter layer on the mesofauna densities. Depending on the physical factors, there are years of high and others with low populations. Extremely wet years could also exert an influence on the soil mesofauna and studies of long–term periods are recommended. Although there was a tendency for the Acari Non-Oribatida biomass estimated in this study to be lower than in temperate forest, the values are however higher than values recorded for many tropical forests. On the contrary, Oribatida and Collembola biomass were characterized by lower values compared to temperate forests.

Resumo

Foram efetuadas coletas trimestrais da mesofauna (junho/1997 a março/1999), na liteira e no solo de parcelas em policultivo (POA e POC) e em florestas primária (FLO) e secundária (SEC). A maior densidade foi registrada na POC, resultante da maior dominância de Oribatida. As densidades de Oribatida e Collembola foram notavelmente menores no solo mineral do que na serapilheira. A mesma tendência não foi detectada para os outros Acari. Ao contrário dos outros grupos, as maiores densidades de Collembola foram registradas na FLO. Em geral, as maiores densidades foram registradas na serapilheira. Entretanto, diferenças marcantes foram detectadas entre 1997, um ano excepcionalmente seco devido ao fenômeno "El Niño" e com menores registros de densidade, e 1998. Somente em 1997 as densidades na FLO, na POA e na POC foram maiores na camada do solo mineral. O padrão na SEC não foi o mesmo, provavelmente devido à maior quantidade de liteira. Nós hipotetizamos que as diferenças entre 1997 e 1998 foram resultados de: 1) uma reação da mesofauna que migrou para o solo mineral no período extremamente seco em 1997 e 2) uma consequência da redução da liteira que ocorreu em 1997, causando menor densidade da mesofauna. Sobreposto aos fatores microclimáticos, observamos a influência da condição da camada de serapilheira sobre a densidade da mesofauna. Dependendo dos fatores físicos, existe anos de alta e outros com baixa populações, levando à hipótese de que anos extremamente úmidos também podem exercer influência na população da mesofauna e são recomendados estudos de longa duração. A biomassa de Acari (exceto Oribatida), calculada nesse estudo, foi menor do que em floresta temperada, porém, os valores foram maiores que aqueles estimados para outras florestas tropicais. Ao contrário, os valores para Oribatida e Collembola foram menores em comparação com as florestas temperadas.

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Key words

Mesofauna, Acari, Collembola, primary forest, secondary growth, polyculture plantation, vertical migration

1. Introduction

The sustained efficiency of a dystrophic Amazonian forest ecosystem appears to be dependent on the distribution of roots and living organisms in the soil, since it is through them that most of the recycling of nutrients is carried out (CHAUVEL et al. 1987). As management practices have a significant impact on the density and activity of the soil biota, information about these effects on invertebrate populations is needed (ROPER & GUPTA 1995). A contribution to this context is given by several ongoing projects at the Brazilian Agroforestry Research Facility (Embrapa Amazônia Ocidental) within the German-Brazilian Scientific Cooperation Program "Studies of Human Impact on Floodplains and Forest in the Tropics" (SHIFT).

The investigations took place on an abandoned rubber tree plantation (*Hevea brasiliensis*, "Seringueira") which has been used as a polyculture forestry research area since 1992. Originally, the area was cleared of primary rain forest in 1979/1980, and then the rubber tree plantation was abandoned in 1984.

After 1984, the plantation naturally transformed itself into secondary growth through neglect. Using this area as an experiment, the fallow rubber plantation was cultivated (in 1992) with mixed plantings of annual and perennial plants (polyculture systems). In 1997, another project on soil fauna and litter decomposition was established (SHIFT ENV 52 "Soil Fauna and Litter Decomposition in Primary and Secondary Forest and a Mixed Culture System in Amazonia"), closely related to the existing SHIFT projects in Manaus. Parameters, such as the quantity and quality of the litter produced in the systems, the decomposition rates, and the abundance, biomass and respiration of microorganisms and soil animals, were simultaneously and comparatively studied in the primary and secondary forest and in one polyculture system (HÖFER et al. 2001).

Although there is a considerable amount of literature concerning the spatial and seasonal distribution of the invertebrates in the soil, most of these studies are restricted to a short-term period and limited to macrofauna. Therefore, our study was developed over a period of two years and describes for the first time the density and biomass of the most abundant groups of the soil mesofauna (Acari Non-Oribatida, Acari Oribatida and Collembola) in Amazonia. Comparing the three forestry systems involved, our principal research questions were 1) What are the density and biomass of these groups? 2) Does the difference of the physical factors between the dry and wet periods exert influences on the density and biomass of the mesofauna? 3) Does the climatic changes during exceptionally dry years exert some influence on the densities of the mesofauna in relation to the litter or mineral soil? 4) Are the mesofauna groups studied here sensitive to the anthropogenic action?

2. Study sites, materials and methods

The study area belongs to the agroforestry research station of "Embrapa Amazônia Ocidental", located close to the city of Manaus, Amazonas, Brazil (3°8'S, 59°52'W). The previously mentioned plantation was divided into 90 experimental plots of 32 x 48 m each (BECK et al. 1998, LIEBEREI & GASPAROTTO 1998, VOHLAND & SCHROTH 1999). In the polyculture system IV (a plantation with four tree species), two plots (POA and POC) were sampled in comparison with one 40 x 40 m plot in a secondary (SEC) forest and another of the same size in a primary (FLO) forest. All plots were situated within a distance of less than 300 m of each other. The plot named POC was located close to the edge of the primary forest and the one situated at POA was close to a secondary forest. The entire area has soils of the yellow clayey latosol (Oxisol) type.

Soil fauna densities were assessed every three months, from June 1997 to March 1999 (eight sample events). At every sample event, 10 random samples were taken from each of the polyculture plantations POA and POC and 20 from the primary (FLO) and secondary (SEC) forested areas. As we did not sample replicates of the growth areas, our analyses show only the differences between the single plots. The samples were taken following a 1 m grid of lines marked at each plot. Soil samples were taken in the field with a split corer (steel cylinder, diameter 6.4 cm, corresponding to 0.0032 m^2), to a depth of 5 cm. Each sample was divided into two sub-samples: the litter layer and the mineral soil. The Kempson process was used to extract the mesofauna from the samples. To obtain biomass values, additional live material was collected with Berlese-Tullgren extracts of the soil and litter layers in the experimental area. The animals were selected and weighed with an electronic microbalance. The animals were then dried at 60°C for 72 hours to obtain their dry weight. A representative number of individuals belonging to each group was then used to get an average individual weight. The biomass of the specified taxa was obtained by multiplying the number of individuals per m^2 with the average individual weight.

The data set of daily values of maximum, minimum, and average soil temperature, air humidity, evapotranspiration and rainfall was obtained from the climatic station of the Embrapa Amazônia Ocidental for January 1996 through April 1998 and computed by MARTIUS et al. (2000). This station is a standard climatic station. Monthly averages were computed on the basis of these daily values. The saturation deficit was calculated from the air temperature and relative humidity according to the "Magnus formula" (D'ANS-LAX 1967). The microclimate was measured with data loggers in 6 different sites. Due to technical reasons (battery life duration), the data was obtained in three subsets: August 1997 to March 1998, May 1998 to November 1998, and November 1998 to April 1999. Using the small data loggers (Stowaway XTI Internal/External Temperature Logger), we recorded the temperature in the litter layer above the soil and in the soil to a depth of 5 cm. The relative air humidity was recorded at approximately 10 cm above the soil (on the litter surface) (MARTIUS et al. 2000).

3. Results

3.1 Climatic factors

Rainfall occurrence is shown in figure 1. The rainfall, the average minimum and maximum air temperature, and the relative air humidity measured at the Embrapa weather station, all show that 1997 was a strong El Niño (ENSO) year. This is also reflected in the microclimate of the study sites, where the maximum and average air and soil temperatures were highest in September and October of 1997. Minimum air temperatures were elevated in the subsequent period, from October 1997 to May 1998. The relative humidity of the air was extremely low in September 1997, and evapotranspiration and the calculated saturation deficit were very high. Litter temperatures in FLO, SEC, POC were similar, but in POA, they averaged about 2°C higher. The highest maximums were recorded in POA, showing that the microclimatic conditions are much more variable and unpredictable there than in the other plots. Soil temperatures were lowest in FLO, higher in SEC, and still higher in POA. In FLO, the soil temperature almost equaled the temperature of the litter layer, whereas soil temperatures in POA were considerably lower than the litter temper-

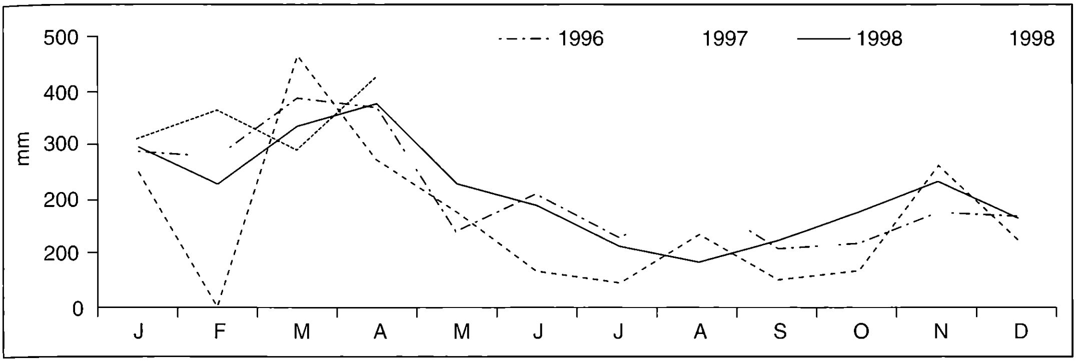

Figure 1. Rainfall results of the station at the Embrapa Amazônia Ocidental (monthly sums) during the study period.

atures. Air humidity of all sites was lowest in September/October 1997 In the other months, it almost always stayed near 100% in FLO, SEC and POC, but was much lower in POA (MARTIUS et al. 2000).

3.2 Density, biomass and group compositions

The values obtained for the wet and dry individual weight of Acari Oribatida, Acari Non-Oribatida and Collembola are summarized in table 1 and compared with the results of other authors for temperate regions. These values are the first to be obtained for the Central Amazon region.

Contrary to what was expected in terms of total values of the mesofauna in the litter layer and mineral soil during the 21-month sampling period, the highest densities and biomass of the mesofauna was not observed in FLO, but in the anthropogenic systems. The total densities of mesofauna decreased in the following order: POA > SEC > POC > FLO (tab. 2).

In FLO, SEC and POC, the total densities of Acari Non-Oribatida were lower than those registered for POA (5,725 ind/m^2). The difference in values between the highest density in POA and the lowest in FLO (5,0 ind/m^2) was only 12.6% (tab. 2).

The increase of the density of Acari Oribatida in POC (12,722 ind/m^2) was only 1.2% higher than that registered for SEC (12,562 ind/m^2), meaning that they were almost similar. The densities in POC and SEC were 18.5% higher than the value obtained in FLO (10,398 ind./m^2). Remarkably, the difference in values obtained between the highest density in POA (23,371 ind/m^2) and the lowest in FLO, was as high as 44.5% (tab. 2). Following an inverse pattern from those registered for Acari Oribatida and Non-Oribatida, Collembola was clearly higher in the primary forest (FLO), with a value of 3,296 ind/m^2 and was 37, 28 and 24% higher than the values registered in POC, POA and SEC respectively (tab. 2).

Comparing the values of the litter layer added to the mineral soil, the relative dominance of Acari Oribatida over the Acari Non-Oribatida and Collembola was very high, the minimum value reaching 64% in FLO to the maximum of 82% in POA. The lowest values registered for Collembola in POA and FLO varied between 5 and 14% respectively (tab. 2).

3.3 Seasonal fluctuations and vertical distribution of the mesofauna in the soil profile

Analyzing separately the two layers of the samples in the four plots, the dominance of Acari Oribatida (D %, tab. 2) in relation to the other two groups was highest in POA (77.6 and 68% in the litter and mineral soil, respectively). In FLO, SEC and POC, the density of Acari Oribatida was 54% of the mesofauna in both layers.

Table 1. Individual weight (the standard deviation is represented in parentesis) of Acari Non-Oribatida, Acari Oribatida and Collembola.

		Acari Non-Oribatida	Acari Oribatida	Collembola
Wet Weight (mg)	This study	0.04092 (0.06291)	0.08422 (0.1018)	0.06316 (0.04981)
	Other studies		0.11675** 0.053*	
Dry Weight (mg)	This study	0.02111 (0.03790)	0.03373 (0.04155)	0.02059 (0.04245)
	Other studies	0.087*	0.0295**	0.027*

* PETERSEN (1892); **LUXTON (1975)

Table 2. Mean density (ind/m^2) and biomass (dry weight mg/m^2) with standard error of Acari Non-Oribatida, Acari Oribatida and Collembola in the litter layer and mineral soil at FLO, SEC (n = 20), POA and POC (n = 10) in eight trimestral sampling periods. D (%) = dominance of each group in relation to the total catch and IP (%) = increased percentage of the highest density value compared to the lowest between the two soil profiles.

		Litter			Mineral Soil			Litter and Mineral Soil	Total Litter + Mineral Soil		
		Density	Biomass	D (%)	Density	Biomass	D (%)	IP (%)	Density	Biomass	D (%)
FLO	Acari Non-Oribatida	2484.6 (349.1)	52.4 (7.4)	24	2516.0 (433.3)	53.1 (9.1)	29	1.2	5000.6	105.5	22
	Acari Oribatida	5727.7 (698.2)	193.2 (23.5)	57	4670.9 (955.1)	157.5 (32.2)	54	18.4	10398.6	305.7	64
	Collembola	1905.4 (561.0)	39.2 (11.5)	19	1390.3 (213.1)	28.6 (4.4)	17	27	3295.7	64.0	14
	Total								18694.9	475.2	
SEC	Acari Non-Oribatida	2987.9 (492.1)	63.0 (10.3)	21	2014.0 (354.0)	42.4 (7.4)	35	32.6	5001.9	105.6	18
	Acari Oribatida	9405.1 (1980.8)	317.2 (66.8)	66	3157.1 (523.8)	106.5 (17.7)	55	66.4	12562.2	423.7	73
	Collembola	1914.9 (544.2)	39.4 (11.2)	13	592.8 (145.5)	12.2 (3.0)	10	69	2507.7	51.6	9
	Total								20071.8	580.9	
POA	Acari Non-Oribatida	2997.7 (732.1)	62.3 (15.4)	14.5	2737.2 (843.1)	57.8 (17.8)	25	8.7	5724.9	120.1	13
	Acari Oribatida	16030.3 (5235.3)	540.7 (176.6)	77.6	7340.6 (1893.1)	247.6 (63.8)	68	54.2	23370.9	788.3	82
	Collembola	1621.3 (598.9)	33.4 (12.3)	7.8	754.3 (114.8)	15.5 (2.4)	7	53.5	2375.6	48.9	5
	Total								31471.4	957.3	
POC	Acari Non-Oribatida	2480.6 (658.9)	52.4 (13.9)	22	2535.0 (260.9)	53.5 (5.5)	31	2.1	5015.6	105.9	18.5
	Acari Oribatida	7935.4 (1862.5)	267.7 (62.8)	68	4786.1 (603.5)	161.4 (20.3)	58	39.7	12721.5	429.1	74
	Collembola	1184.6 (318.4)	24.4 (6.5)	10	895.6 (265.1)	18.5 (5.5)	11	24.3	2080.2	42.9	7.5
	Total								19817.3	577.9	

Table 3. Mean density (ind./m^2) and biomass (mg/m^2) of the Acari Non-Oribatida, oribatid mites and Collembola in the four systems, during the dry (July, September/1997, June and September/1998) and wet (December/1997, March/1998, December/1998 and March/1999) months. The standard errors are given in parenthesis.

	Litter Density		Biomass		Soil Density		Biomass	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Acari Non-Oribatida								
FLO	1881.80 (436.67)	1976.03 (456.70)*	39.72 (9.22)	41.71 (9.64)	3374.81 (879.56)*	3238.50 (519.93)	71.24 (18.57)	68.36 (10.98)
	2566.10 (363.77)*	1601.87 (407.60)	54.17 (7.68)	33.82 (8.60)	3390.36 (702.76)	4261.28 (831.59)*	71.57 (14.84)	89.96 (17.55)
	3530.33 (453.72)*	3094.87 (683.88)	74.52 (9.58)	65.33 (14.44)	793.16 (178.36)	2208.40 (557.74)*	16.74 (3.77)	46.62 (11.77)
	1213.06 (277.20)	4012.44 (702.04)*	25.61 (5.85)	84.70 (14.82)	1321.93 (316.62)	1539.66 (284.07)*	27.91 (6.68)	32.50 (6.00)
SEC	1586.31 (404.86)	2037.33 (496.69)*	33.49 (8.55)	43.01 (10.49)	1726.28 (354.27)	3374.81 (483.07)*	36.44 (7.48)	71.24 (10.20)
	2037.33 (330.47)	3950.23 (601.32)*	43.01 (6.98)	83.39 (12.69)	2566.10 (690.70)*	1788.49 (397.87)	54.17 (14.58)	37.76 (8.40)
	4634.53 (923.23)*	3856.92 (636.41)	97.83 (19.49)	81.42 (13.43)	917.57 (182.59)	3234.84 (468.69)*	19.37 (3.85)	69.29 (9.89)
	1259.72 (358.55)	4541.21 (924.20)*	26.59 (7.57)	95.87 (19.51)	590.98 (114.84)	1912.91 (329.55)*	12.48 (2.42)	40.38 (6.96)

POA	1181.96 (296.54)	3545.88 (622.26)*	24.95 (6.26)	74.85 (13.14)	2146.19 (410.10)	7153.97 (1006.30)*	45.31 (8.66)	151.02 (21.24)
	1275.27 (271.26)	6065.32 (1515.40)*	26.92 (5.73)	128.04 (31.99)	5536.55 (826.73)*	590.98 (189.63)	116.88 (17.45)	12.48 (4.00)
	3390.36 (618.15)*	2830.48 (471.10)	71.57 (13.05)	59.75 (9.94)	1150.86 (153.96)	2923.79 (437.58)*	24.29 (3.25)	61.72 (9.24)
	217.73 (73.68)	5474.34 (701.06)*	4.60 (1.56)	115.56 (14.80)	870.92 (269.97)	1923.79 (437.68)*	18.39 (5.70)	32.17 (7.37)
POC	1959.56 (389.39)*	870.92 (238.24)	41.37 (8.22)	13.89 (5.03)	2674.96 (388.22)	2892.69 (472.92)*	56.47 (8.20)	61.06 (9.98)
	870.92 (156.56)	3676.98 (1057.48)*	18.39 (3.30)	75.51 (22.32)	2830.48 (271.26)	3297.05 (640.98)*	59.75 (5.73)	69.60 (13.53)
	995.33 (256.65)	1430.79 (323.25)*	21.01 (5.40)	30.20 (6.82)	1026.44 (296.99)	2270.61 (360.73)*	21.67 (6.27)	47.93 (7.62)
	4386.69 (1866.24)	5754.28 (1062.04)*	92.58 (39.38)	121.47 (22.42)	3203.73 (1193.49)*	2083.98 (251.95)	67.63 (25.19)	43.99 (5.32)
Oribatida								
FLO	2814.93 (569.29)	5946.39 (966.52)*	94.95 (19.20)	200.57 (32.60)	5023.33 (948.90)	10648.61 (2054.65)*	169.44 (32.01)	359.18 (69.30)
	5147.74 (933.26)	6345.26 (1549.71)*	173.63 (31.48)	214.03 (52.27)	4930.02 (505.22)	5381.03 (606.38)*	166.29 (17.04)	181.50 (20.45)
	8895.80 (1554.31)*	6127.53 (1109.41)	300.06 (52.43)	206.68 (37.42)	2612.75 (464.87)	3732.50 (460.80)*	88.13 (15.68)	125.90 (15.54)
	3343.70 (642.18)	7200.62 (1201.98)*	112.78 (21.66)	242.88 (40.54)	2146.19 (493.30)	2892.69 (322.38)*	72.39 (16.64)	97.57 (10.87)
SEC	2519.44 (571.27)	5038.88 (843.30)*	84.98 (19.27)	169.96 (28.44)	1632.97 (258.15)	5925.35 (634.44)*	55.08 (8.71)	199.86 (21.40)
	4992.22 (900.78)	18102.64 (5093.05)*	168.39 (30.38)	610.60 (171.79)	2534.99 (392.33)*	2130.64 (233.72)	85.51 (13.23)	71.87 (7.88)
	14370.14 (2368.69)*	13079.32 (2184.49)	484.70 (79.90)	441.17 (73.68)	2177.29 (359.64)	4805.60 (719.79)*	73.44 (12.13)	162.09 (24.28)
	5521.00 (1219.56)	11617.42 (1882.33)*	186.22 (41.14)	391.86 (63.49)	3359.25 (1424.96)*	2690.51 (355.56)	113.31 (48.06)	90.75 (11.99)
POA	2052.88 (197.27)	8304.82 (1633.12)*	69.24 (6.65)	280.12 (55.09)	7465.01 (3237.79)	12223.95 (1882.91)*	251.79 (109.21)	412.31 (63.51)
	3328.15 (1053.81)	30793.16 (2787.47)*	112.26 (35.54)	1038.65 (94.02)	5194.40 (478.57)*	3794.71 (922.59)	175.21 (16.14)	128.00 (31.12)
	17138.41 (2137.81)	44852.26 (19368.63)*	578.08 (72.11)	1512.87 (653.30)	3639.19 (643.37)	18413.69 (6816.91)*	122.75 (21.70)	621.09 (229.93)
	8087.09 (1369.22)	13685.85 (1340.66)*	272.78 (46.18)	461.62 (45.22)	4696.73 (692.77)*	3297.05 (543.91)	158.42 (23.37)	111.21 (18.35)
POC	4914.46 (1288.66)*	3390.36 (956.15)	165.76 (43.47)	114.36 (32.25)	4136.86 (720.61)	7993.78 (942.90)*	139.54 (24.31)	269.63 (31.80)
	2301.71 (324.91)	15054.43 (3668.66)*	77.64 (10.96)	507.79 (123.74)	4385.69 (419.17)*	4292.38 (883.91)	147.93 (14.14)	144.78 (29.81)
	16205.29 (5765.89)*	5069.98 (725.07)	546.60 (194.48)	171.01 (24.46)	3545.88 (1185.87)	6842.92 (1573.43)*	119.60 (40.00)	230.81 (53.07)
	6656.30 (1608.30)	9891.14 (1326.47)*	224.52 (54.25)	333.63 (44.74)	4012.44 (873.30)*	3079.32 (480.14)	230.81 (53.07)	103.87 (16.19)
Collembola								
FLO	777.60 (202.46)	841.64 (326.01)*	16.01 (4.17)	17.33 (6.71)	1741.84 (308.08)*	933.13 (279.29)	35.86 (6.34)	19.21 (5.75)
	1244.17 (304.43)*	870.92 (240.61)	26.52 (6.27)	4.95 (4.95)	1741.84 (314.63)*	1010.98 (219.80)	35.86 (6.48)	20.81 (4.53)
	4650.08 (876.13)*	2317.26 (571.97)	95.75 (18.04)	47.71 (11.78)	1135.30 (361.95)	1990.67 (553.84)*	23.38 (7.45)	40.99 (11.40)
	575.43 (135.50)	3048.21 (476.27)*	11.85 (3.16)	62.76 (9.79)	419.81 (91.03)	2149.16 (306.01)*	8.65 (1.87)	44.19 (6.30)
SEC	451.01 (160.32)	590.98 (216.32)*	9.29 (3.30)	12.17 (4.45)	342.16 (95.47)*	202.18 (88.19)	7.04 (1.91)	4.16 (1.86)
	1041.99 (289.63)	4136.86 (863.14)*	21.45 (5.34)	85.18 (17.77)	388.80 (138.87)	1305.38 (231.89)*	8.01 (2.86)	26.90 (4.97)
	2814.93 (664.62)*	1804.04 (252.90)	57.96 (13.68)	37 16 (5.21)	684.29 (309.07)	1088.65 (301.48)*	14.09 (6.36)	22.42 (6.21)
	513.32 (130.17)	3965.79 (888.94)*	10.57 (2.68)	81.66 (18.30)	186.63 (47.33)	544.32 (146.02)*	3.84 (0.97)	11.21 (3.01)
POA	279.94 (89.49)	435.46 (284.32)*	5.76 (1.84)	8.97 (5.85)	1026.44 (540.79)	1275.27 (646.20)*	21.13 (11.13)	26.26 (13.31)
	497.67 (127.83)	2021.77 (391.06)*	10.25 (2.63)	41.63 (8.05)	777.60 (304.50)*	217.73 (80.65)	16.01 (6.27)	4.48 (1.66)
	4416.80 (853.60)*	1026.44 (260.34)	90.94 (17.58)	21.13 (5.36)	746.56 (143.67)	808.71 (205.28)*	15.37 (2.96)	16.65 (4.23)
	311.04 (118.22)	3981.34 (670.17)*	6.40 (2.43)	81.98 (13.80)	435.46 (143.67)	746.50 (276.66)*	8.97 (2.96)	15.37 (5.70)
POC	342.15 (110.94)	1150.86 (348.61)*	7.04 (2.28)	23.70 (7 18)	1026.44 (298.79)	1461.90 (227.27)*	21.13 (6.15)	30.10 (4.68)
	456.56 (123.77)	1524.11 (400.82)*	9.61 (2.55)	31.38 (8.25)	93.31 (46.94)	1161.95 (163.28)*	1.82 (0.97)	24.34 (3.36)
	342.15 (197.95)	1306.38 (294.72)*	7.04 (4.08)	26.90 (6.06)	0.00 (0.00)	1399.69 (218.10)*	0.00 (0.00)	28.82 (4.49)
	1275.27 (230.56)	3079.32 (759.39)*	26.26 (4.75)	63.40 (15.64)	62.21 (29.33)	1959.56 (639.18)*	1.28 (0.60)	40.35 (13.16)

* Highest mean density value comparing dry and wet periods at each surface layer.

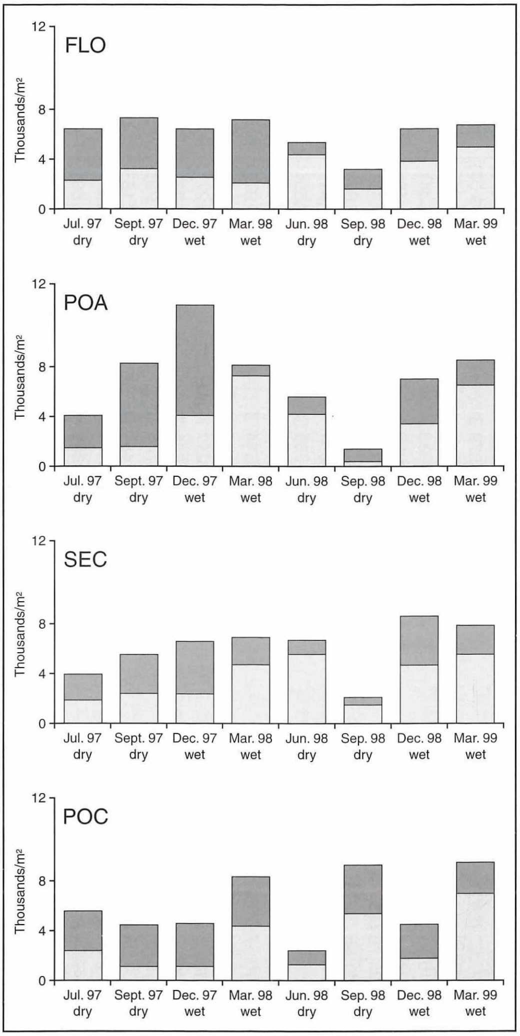

Figure 2. Mean density (Ind./m^2) of Acari Non-Oribatida in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n = 20), Secondary Forest (SEC; n = 20) and the Polyculture system (POA and POC; n = 10 each).

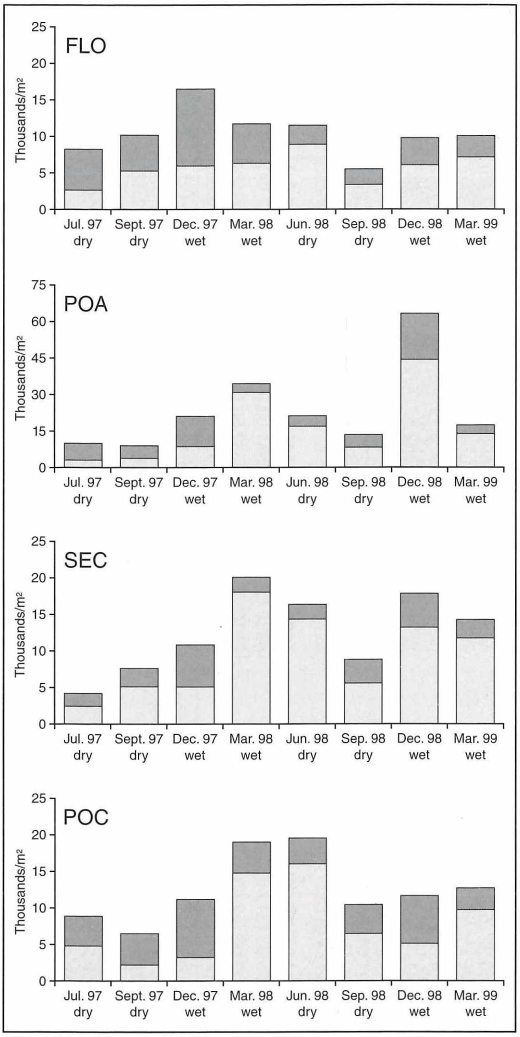

Figure 3. Mean density (Ind./m^2) of Acari Oribatida in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n = 20), Secondary Forest (SEC; n = 20) and the Polyculture system (POA and POC; n = 10 each). Notice differences in scale of Ind./m^2 for POA.

The density of all of the mesofauna groups was higher in the litter layer than in the soil layer (tab. 2), the only exception was for Acari Non-Oribatida in FLO and POC, where the densities for the mineral soil were higher. Notably, the total density of Acari Non-Oribatida in the four plots were almost similar. The difference between the values, for the mineral soil and the litter layer, did not exceed 1.2% in FLO and 2.1% in POC. The different values obtained in the soil and litter layers continued even when the densities in the litter layer increased, reaching 32.6 and 8.7% in SEC and POA, respectively (tab. 2, fig. 2). In sharp contrast, the pattern observed for the decomposers groups shows their clear preference for the litter layer. These differences were more apparent in SEC and POA. For Acari Oribatida and Collembola, the largest difference between the soil and litter layers (SPD %) was obtained in SEC (66.4 and 69%, respectively) and POA (54.2 and 53.5%, respectively) while the lowest was in FLO (18 and 27%, respectively) (tab. 2, figs 3 and 4).

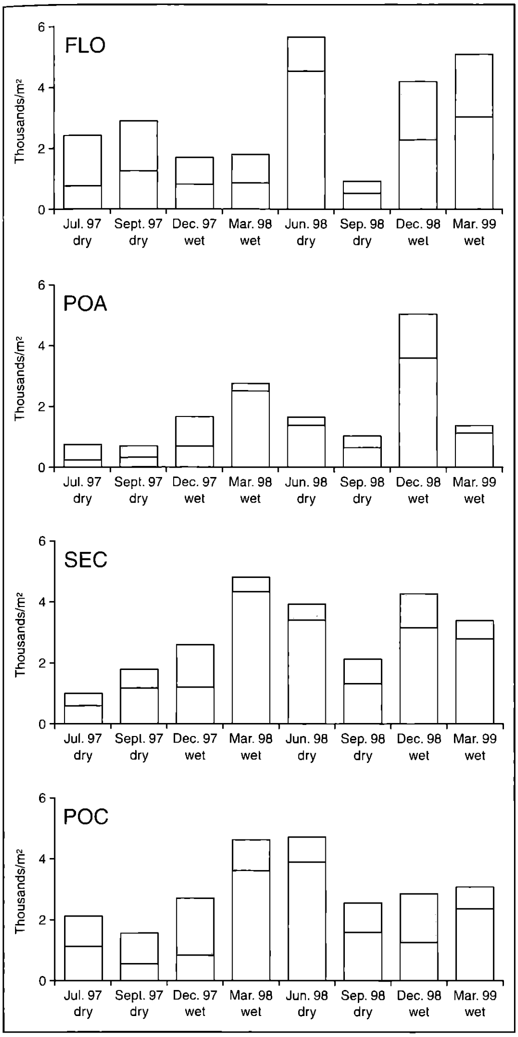

Figure 4. Mean density (Ind./m^2) of Collembola in the litter (light bars) and soil (dark bars) in a Primary Forest (FLO; n= 20), Secondary Forest (SEC; n = 20) and in the Polyculture system (POA and POC; n = 10 each).

For both the litter layer and mineral soil, and for all the mesofauna groups, the highest density and biomass values were generally during the wet season (tab. 3; figs 2, 3 and 4). Lower values coincided with the lower rainfall occurring in the area during the driest period of June - October (fig. 1). This was also reflected in the microclimate of the study sites (soil temperature, relative humidity of the air, litter and soil temperatures).

3.4 Differences between 1997 and 1998

A clear pattern in all mesofauna groups was the higher densities in the mineral soil during the extremely dry year of 1997, principally in FLO, POA and POC (tab. 3, figs 2, 3 and 4). One exception was registered in SEC, but only for Acari Oribatida and Collembola. In this area, the pattern for Acari Non-Oribatida was the same observed for the other groups during 1997 Therefore, during 1998 and 1999, the ratio soil/litter in 1997 was inverted due to high densities of the mesofauna in the litter layer for all of the plots. In the litter layer, the densities of the Acari Oribatida were higher principally in the SEC, POA and POC (tab. 3, fig. 3) and the highest densities of Collembola were detected at FLO and SEC (tab. 3, fig. 4).

Comparing 1997 and 1998, the total mesofauna density increased 29.7% in 1998. The total amount of animals in the litter and mineral soil also differed strongly. In 1998, the density in the litter layer increased 60%, while in the mineral soil a 28% of reduction was detected (tab. 4, fig. 5).

For each group, it can be clearly seen that densities in the litter layer of 1998 were higher than in the soil fraction and that densities in the soil fraction of 1997 were higher than that in the litter layer. In 1998, the density of Acari Non-Oribatida in the litter layer increased 29.4%. Therefore, in 1997, the density in the mineral soil was almost twice as that registered in 1998. The same tendency was also observed in the two decomposers groups. In 1998, the number of oribatid mites in the litter layer increased 66%. In 1997, the density obtained in the mineral soil was almost 17% greater than that of 1998. In 1998, the number of Collembola in the litter layer increased by 62% and, in 1997, the densities in the mineral soil increased by 18.6% (tab. 4, fig. 5).

We detected the highest amount of litter (mean dry weight) in the year of 1998, principally in POC and SEC, whose values were 64 and 39%, respectively, higher than 1997 (tab. 6). In the mineral soil the differences in mean dry weight between 1997 and 1998 did not exceed 24%.

The highest litter and soil temperatures were recorded in POA and there was a general tendency for temperatures to be higher in 1997 than in 1998 in each plot (fig. 6).

3.5 Biomass estimates

The values obtained for the biomass estimates of Acari Oribatida, Acari Non-Oribatida and Collembola in main biomes are summarized in table 5. Comparing the four plots of this study, the total biomass (dry weight) of the soil mesofauna varied between the minimum of 475 mg/m^2 and the maximum of 957 mg/m^2 in FLO and POA, respectively. The values obtained for SEC (582 mg/m^2) and POC (578 mg/m^2) were very similar. Comparing the areas of this study with the other Amazonian forests, the lowest values of the mesofauna were registered at the flooded forests of várzea and igapó (191 and 287 mg/m^2, respectively). For Acari Oribatida and Acari Non-Oribatida, the values obtained for the SEC (424 and 106 ind/m^2, respectively) were almost similar to that registered in other secondary forest areas (429 and 96 ind/m^2) whose values were the median of the results for five plots of 38 x 42 m at the same experimental area of our study. Comparing the values obtained for central

Table 4. Differences in the years 1997 and 1998 (June/July, September and December) of the mesofauna mean densities (ind./m^2) in FLO, SEC, POA and POC. IP (%) represents the increased percentage of the highest value compared to the lowest between the two years at each soil profile.

	Litter layer			Mineral soil			Total Litter + Mineral Soil		
	1997	1998	IP (%)	1997	1998	IP (%)	1997	1998	IP (%)
Acari Non-Oribatida	21,789	30,841	29.4	40,906	20,513	49.9	62,695	51,354	18.0
Acari Oribatida	50,752	149,347	66.0	72,095	59,984	16.8	122,847	209,331	41.0
Collembola	8,110	21,353	62.0	11,011	8,958	18.6	19,121	30,311	36.9
Total	80,651	201,541	60.0	124,012	89,455	28.0	204,663	290,996	29.7

Table 5. Biomass (mg dry weight/m^2) estimates of Acari and Collembola in main biomes (in parenthesis the percentage of each group in relation to the total mesofauna). Values of the columns 1 to 7 were extracted from Luxton (1975) and represented median values of five or more independent mean biomass estimates. Values of columns 8 and 9 are from Petersen (1982b). Values for Oribatida in columns 10 were extracted from Woas et al. (1982) and for Collembola from Dielmann (1982). Values of the columns 11 to 14 were extracted from our data, 15 and 16 from Franklin et al. (1996) and of the column 17 from Santos (2000; median values of five parcels of 38 x 42 m at the same experimental area of Embrapa).

	Oribatida	Non-Oribatida	Acari (in toto)	Collembola	TOTAL
01 - "tundra"	60 (25)	30 (12)	90	150 (63)	240
02 - temperate "grassland"	110 (37)	100* (33)	120*	90 (30)	300
03 - tropical "grassland"	20* (22)	60* (67)	80*	10* (11)	90
04 - temperate coniferous forest	450 (70)	110* (17)	500	80 (13)	640
05 - temperate deciduous forest (mor soil)	700*		900*	130*	830
06 - temperate deciduous forest (mull soil)	180		300*	110	290
07 - tropical forest			100*	20*	100
08 - temperate forest (mor soil)	400/1000				
09 - temperate forest (mull soil)	100/400				
10 - temperate forest (moder beech wood soil)	300/700			340	
11 - tropical primary forest (FLO)	306 (64)	105 (22)	411	64 (14)	475
12 - tropical secondary forest (SEC)	424 (73)	106 (18)	530	52 (9)	582
13 - tropical polyculture system (POA)	788 (82)	120 (13)	908	49 (5)	957
14 - tropical polyculture system (POC)	429 (74)	106 (18)	535	43 (8)	578
15 - tropical flooded forest ("várzea")	156	35	191		191
16 - tropical flooded forest ("igapó")	266	21	287		287
17 - tropical secondary forest	429	96	525	97	622

* tentatives values generally based on less than five biomass estimates

Table 6. Mean dry weight (mg) and standard deviation (parenthesis) of the litter and mineral soil in the study sites in the years 1997 and 1998 (June/July, September and December). IP (%) represents the increased percentage of the highest value compared to the lowest between the two years at each soil profile.

	Litter			Mineral Soil		
	1997	1998	IP (%)	1997	1998	IP (%)
FLO	10.60 (3.47)	15.03 (4.52)	29	109.31 (14.56)	83.51 (8.05)	24
SEC	13.02 (4.37)	21.28 (6.27)	39	109.30 (10.23)	98.30 (7.57)	10
POA	12.89 (2.67)	15.43 (5.70)	16	103.09 (8.06)	96.11 (11.92)	7
POC	6.83 (2.60)	18.95 (6.24)	64	103.03 (8.39)	98.28 (3.39)	5
TOTAL	11.16 (4.24)	17.83 (6.16)	37	107.16 (11.46)	93.02 (10.99)	13

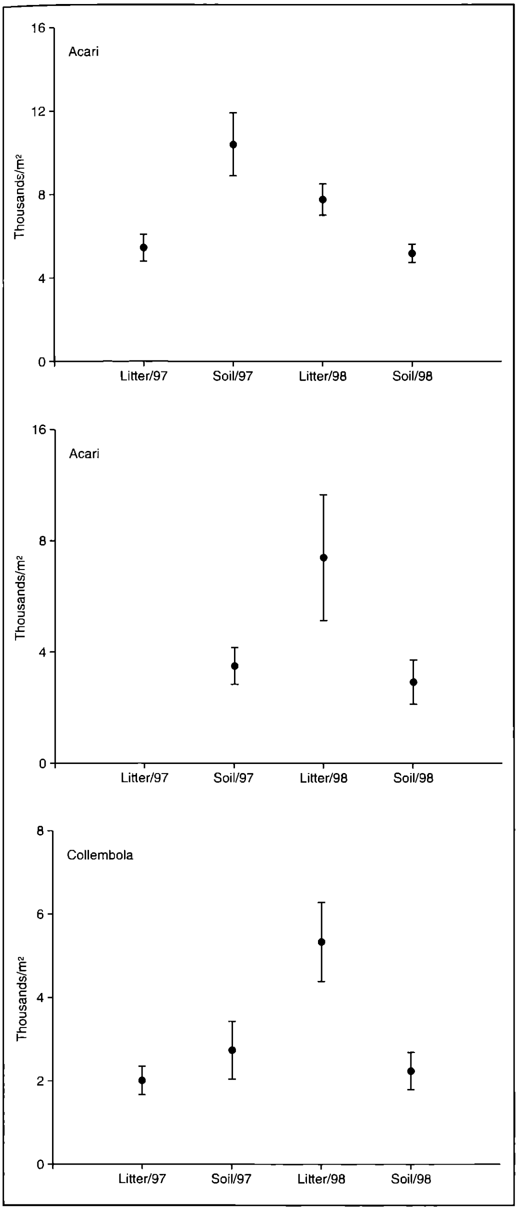

Figure 5. Comparison of the mean density with errors bars of Acari Non-Oribatida, Acari Oribatida and Collembola in FLO, SEC, POA and POC at each soil profile (litter and mineral soil) during the period of June/July, September and December of 1997 and 1998. Notice diference of scale.

Amazon region and even for the temperate coniferous forest, the highest difference of the Acari Oribatida' dominance in relation to the other mesofauna groups was obtained at POA (82%).

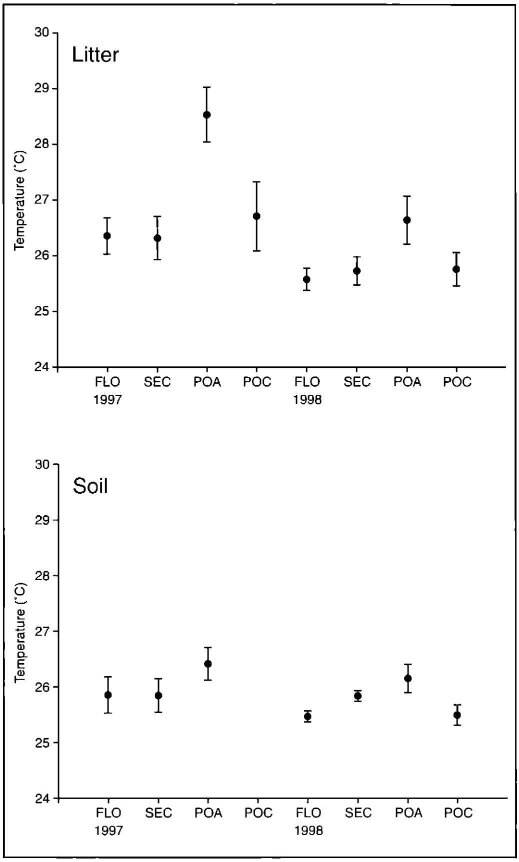

Figure 6. Microclimate measurements with data loggers in the study sites. Litter and mineral soil monthly avarage temperatures with errors bars in 1997 (August, September and December) and 1997 (July, September and December). Data extracted from Martius et al. (2000). Measurement for POC (soil) in 1997 was not available.

4. Discussion

Contrary to our expectation, mesofauna densities were higher in the polyculture POA than in the relatively undisturbed FLO. This is situated at the northwestern extremity of the experimental area and does not receive much shading from the neighboring plantations, nor from the adjacent secondary growth. The microclimate at the soil surface of this plot therefore was much harsher than in the secondary and primary forests (MARTIUS et al. 2000). All these factors resulted in extreme abiotic conditions and contributed to a different annual cycle to that recorded in POC, which is situated near a primary forest and received strong shading from the directly neighboring primary forest. The difference in soil mesofaunal density between POA and POC might be also explained by the more extreme microclimatic conditions in POA (Höfer et al. 2001).

The greatest relative dominance of the Acari Oribatida in relation to the other groups of the mesofauna in POA, point to this group as being principally responsible for the greatest mesofauna density of this plot. A few dominant Acari Oribatida species, mainly *Archegozetes longisetosus* (Aoki, 1965) occurs sporadically, but in great aggregations in Central Amazon region (Oliveira & Franklin 1989). Unfortunately, the Acari Oribatida of our mesofauna study were not identified at species level. Another experiment in the same plots investigated, litterbags of three mesh sizes (1 cm, 250 µm and 20 µm) were filled with a "standard litter" (*Vismia guianensis*) at the end of the rainy season of April/1988 and were implanted in the plots. The mesofauna in these litter bags were sampled after 26, 58, 111, 174, 278 and 350 days from the beginning of the experiment (Beck et al. 1998). According to the results obtained by Hayek (2000), the total mean density of *A. longisetosus* was extremely high in POA (44.85 individuals), followed by SEC, FLO and POC, with 14.25, 1.3 and 0,4 individuals, respectively. Also, in POA, more evidence of aggregation for this specie was reported, as 45% (20.25 individuals) of the total obtained were concentrated in the second period.

Our results for the dominance of the three groups of the mesofauna (POA>SEC>POC>FLO) showed exactly the opposite pattern of dominance obtained for the macrofauna by Höfer et al. (2001), over all eight sampling periods. They reported the macrofauna in the following gradient of dominance: FLO (4,866 ind/m^2), POC (4,266 ind/m^2), SEC (3,769 ind/m^2) and POA (3,745 ind/m^2). Predatory forms made up between 46 and 53% of the total arthropod macrofauna. Also, they reported that the macrofauna density in POA was 23% lower than the values registered in FLO, where the predators were more numerous (53%) and dominated by the Pseudoscorpionida, Diplura, Formicidae and Araneae. Based on these results, we would hypothesise that the relative abundance of the mesofauna density could be explained by the results for macrofauna. The highest densities of macro-predators in plots of lowest mesofauna densities (POC and FLO) suggest that the macropredators could have acted as controllers of the mesofauna abundance. However, our results showed that the highest density of Collembola was obtained in the primary forest (FLO), whose value (3,296 ind/m^2) was 37, 28 and 24% higher than the values recorded in POC, POA and SEC, respectively. This result does not conform with the hypothesis of a high level of predation by the macropredators in plots where they were more abundant, probably because Collembola being very mobile is less susceptible to predation than other mesofauna group. It is quite interesting to observe that Collembola responds differently from the other groups of mesofauna under similar conditions. This is a reflection of the differences in the relative contribution of each of the components of biotic (predation) and abiotic (microclimate) factors operating in each plot to fluctuations in densities of each taxonomic group of the mesofauna. In this study, predation and extreme microclimate have been identified as two majors factors that could have affected mesofauna densities. Also, we can not eliminate the hypothesis that the increased dominance of the oribatid mites caused by of one or more species, like *A. longisetosus*, that became dominant in the anthropogenic plots, could explain our results.

According to Lavelle et al. (1992), the possibility of maintaining or improving soil fertility by manipulating the activities of soil fauna needs to be explored. An enhanced knowledge of the biology and dynamics of soil colonization by populations that are adaptable to relatively harsh ecological conditions is required. In the case of agroecosystems and soil submitted to rehabilitation techniques, the perspectives for the management of soil biodiversity is to maintain key functional groups. This study revealed differences among the mesofauna groups. The density of the two decomposers groups, the Acari Oribatida and Collembola were notably lower in the mineral soil, than in the litter layer. For the Acari Non-Oribatida, the same tendency was not clearly discernible, probably because of their predatory habit. This made more evident the different responses of different taxonomic groups to the same set of environmental conditions.

This study has shown that the population densities of mesofauna fluctuated greatly between 1997 and 1998. The litter arthropod population was lowest in 1997 probably because of the extreme and exceptional dryness caused by the El Niño Southern Oscillation and also due the reduction of the litter layer in the soil surface.

In a tropical deciduous forest in Panama, a dry season with little rain or a long wet season reduced the numbers of litter arthropods. Arthropod abundance was not as random with respect to years and individual groups of litter animals that showed a persistent pattern of seasonal increase and decrease (Levings & Windsor, 1985). In this study, we detected the same pattern, which means that there are years of high and others with low populations, depending on the effects of the physical factors.

When looking at the distribution of the soil mesofauna over the whole period of our study, it can be seen that densities in the litter layer are generally higher than in the soil fraction. Only in 1997, was the mesofauna density in three of the four plots higher in the mineral soil. This tendency was more accentuated in the polyculture system. The pattern in SEC was not the same for the decomposer groups, the Oribatid mites and

Collembola, probably due to the higher amount of surface litter at this plot. We also observed that the amount of litter in 1997 was relatively lower than in 1998 and that the litter and soil temperatures were higher in 1997, principally in the litter layer.

We hypothesize that the differences between 1997 and 1998 are results of: 1) a possible reaction of the mesofauna that migrated to the mineral soil during the extremely dry period of 1997 and 2) a consequence of the reduction of the litter layer that occurred in 1997, causing lower mesofauna densities. We may also conclude that the mesofauna density showed a relationship with the rainfall occurrence, temperature of the litter and the mineral soil as a possible result of dryness stress during the dry periods. Superimposed on these climatic factors, we evidenced the influence of the amount of litter on the soil surface and the possible effect of predation.

The large influence of the microclimate, at least in extreme climatic years as 1997, or via the extremes in normal years, has a restrictive influence on the soil fauna, and thus, on the decomposition process (MARTIUS et al. 2000). The microclimate is influenced by the cropping system, e.g. shading by the plant canopy, soil cover by litter, etc. In general, the results obtained for the primary forest, not subjected to environmental impact, were the most stable during the study period.

In the central Amazon region, the vertical distribution and abundance of arthropods (meso- and macrofauna) in the soil of a secondary dryland forest in 0-14 cm depth were studied in September/1985 (dry season) (ADIS et al. 1987). According to the authors, the results did not correspond with data from the forest in the seasonal tropics (LEVINGS & WINDSOR 1982, 1984; MERINO & SERAFINO 1978). In more markedly seasonal tropics, the abundance of the animals during the dry season was higher in the mineral subsoil as a response to the decreasing humidity in organic layers (ADIS et al. 1987). Another short-term period study was developed in April/1986 (rainy season) (ADIS et al. 1987). They consequently concluded that neither during the rainy season nor during the dry season was the abundance of arthropods in mineral subsoil higher in response to the changing in organic layers, as reported from forests in the seasonal tropics. The macroarthropod community was investigated in a Neotropical mesothermic rainforest (Ecuador) in September/1987 and February/1998. The results of this short-term period of study showed that the vertical distribution did not change dramatically during the low rainfall period, and no clear evidence of vertical migration was detected. Therefore, a clear tendency concerning population dynamics was observed in the litter and soil layers, with the lowest mesofauna density occurring during the driest periods (SILVA DEL POZO & BLANDIN 1991).

While analyzing the results of other long-term period studies with mesofauna, we detected some indications similar to our results. Seasonal densities and vertical distribution of soil mesofauna were studied in a coffee plantation in the Central Plateau of Costa Rica (1,130 mm) from March 1977 to February 1978 (12 sampling periods). The distribution of Collembola, Protura, Symphyla and Acari was positively correlated with the rainy season. The Acari (not separated into Oribatida and Non-Oribatid groups) prevailed in the upper 5 cm of soil depth independent of the season of the year. The highest abundance of Collembola was detected in the upper 5 cm of soil depth during the rainy season, while during the dry season the highest density was detected in the deeper layers of the soil profile (FRAILE & SERAFINO 1978).

On the contrary, in the central Amazon region, two long-term period studies in the soil of a primary (MORAIS 1985) and secondary forest (RODRIGUES 1985) there was a lower density of arthropods during the rainy season. These studies were made during December/1982–May/1983 with the soil sampled once a month in the 3.5 and 3.5-7cm depth (Kempson extraction). As both authors in their results did not include Acari and Collembola, this is probably the main reason for the differences registered here.

In tropical vertisols (Martinique, French West Indies), changes in arthropod communities indicate a decline in soil quality following agricultural use. During the dry period, this type of soil also is unfavorable to the development of soil animal populations and in particular to Collembola due to physiological dryness (high concentrations of smectites). The litter protected the soil against erosion, offered microhabitats and food to litter-dwelling groups and prevented vertisols from shrinking during dry periods (LORANGER et al. 1999). In Central Amazon, soil and litter-inhabiting fauna depends on litter quantity (HÖFER et al. 1996) and quality and on microclimatic conditions in the specific habitat (HÖFER et al. 2001). Complementary, our results have also revealed that the mesofauna density oscillates between years of extreme and "normal" climatic registers, resulting in migration of the mesofauna to the mineral soil during the extreme driest period. In addition, a more accentuated influence of these factors in the antropogenic system has been observed. Based on these results, we may also hypothesize that the extremely wet years could exert an influence on the soil fauna population. This underscores the need to carry out long-term studies. According to LEVINGS & WINDSOR (1984), the population distributions in tropical areas are the result of interactions among many factors. Physical factors, often assumed to be unimportant in the tropics, can not be disregarded or excluded as contributors to the observed variance in animal and plant distribution.

It is quite possible that not only the amount of litter but also the diversity of leaves available on the soil surface could exert some effect on the soil invertebrate communities. Therefore, the effect of different qualities of litter was tested in the development of the invertebrate community. The experiment took place in 5 plots (30 x 40 m) of secondary forest in Central Amazonia. Four substrata were tested: 1) *Hevea brasiliensis* ("seringueira"), 2) *Carapa guianensis* ("andiroba"), 3) a "mixture" of *Hevea*, *Carapa* and *Vismia* spp. ("lacre", the predominant leaf species on the soil of the secondary forest plots) and 4) the original and more diversified litter layer. The results showed that the density of the selected groups (decomposers, herbivores, predators, social groups and others) in the litter layer did not differ significantly between the four substrata. Analysis of the multidimensional scaling, using the PATN program showed that there was no difference in the fauna composition in the litter and mineral soil between the four treatments (SANTOS 2001). The reduction of the diversity of the leaves did not affect adversely the soil community, principally the Acari and Collembola, that possess a large alimentary spectrum. The author states the possibility that the soil invertebrates could respond in a more favorable way to the reduction of the diversity and amount of resources in the soil than is actually supposed. According to LEBRUN & VAN STRAALEN (1995), the oribatid mites occupy a great variety of habitats, possess a great diversity in morphology and feeding habits, have different ways of reproduction, and above all exhibit complex and diverse life cycles.

Our results for the Acari Oribatida and Collembola individual weights are close to those obtained in other studies and are the first biomass results based on concrete measures for the central Amazon region. The values given in earlier literary works were only estimates. However, since the average individual weights have only been measured on only one occasion, which ignored changes in relative population with the time (PETERSEN 1982a), our results of biomass need to be interpreted with caution. The most recommended procedure would be the estimation for each sampling period of the year in a long-term study.

In our study areas, the Acari Non-Oribatida biomass varied between 105 – 120 ind/m^2) and did not differ much from the temperate forest value estimation (110 ind/m^2; LUXTON 1975). Although there is a tendency for the Acari Non-Oribatida biomass estimated in this study to be lower than in temperate forest, the values are however higher than values recorded for many tropical forests where total Acari are about 100 mg/m^2 as reported by LUXTON (1975). Collembola biomass obtained at FLO (64 mg/m^2), SEC (52 mg/m^2), POA (49 mg/m^2) and POC (43 mg/m^2) were lower than the values estimated for temperate forests that vary between 80 and 340 mg/m^2 (LUXTON 1975, DIELMANN 1982).

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