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On Biomass and Trophic Structure of the Central Amazonian¹ Rain Forest Ecosystem

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ABSTRACT

The importance of litter in the total energy flow dynamics of a central Amazonian rain forest near Manaus, Brazil, is discussed. The study area is located in the hinterland of Manaus between the Rio Negro and the Amazon. Its substrate is Tertiary sediment. The area receives 1771 mm rainfall per year, and the soil is classified as yellow latosol. The forest comprises 93,780 dicotyledonous trees and palms per hectare reaching 38.10 meters in height. Over 500 species of palms and dicotyledonous trees above 1.5 m. in height are identified for a 2000 sq. m. plot. The estimate for fresh living dicotyledonous tree and palm biomass is 939.5 metric tons per hectare consisting of 1.9% leaves, 49.7% stems, 21.3% branches and twigs, and 27.1% roots. Lianas, vascular epiphytes, and parasites are estimated to comprise 46.2 mt/hectare in the fresh state. At the soil surface there are 59 mt/hectare of fresh litter. Living animal biomass is about 200 kg/hectare of which half is soil fauna. The high proportion of soil fauna, the type of humus, the decomposition of litter, the apparent dependence of soil fauna on fungi, and the low nutrient content of litter are all factors which strongly support a consumer food chain based almost entirely on dead organic matter. The fungi play a decisive role in concentrating the otherwise limited nutrient resources.

ECOLOGICAL STUDIES carried out in the Amazon region (Fittkau *et al.* 1969) raised further questions concerning the richness of the Amazonian ecosystems, the distribution of their biomass, and importance of overall as well as trophic-level structure. Additional experience obtained through later fieldwork in Amazonia and the results of our studies in hydrobiology, ecology, landscape ecology, pedology, and terrestrial production indicated the importance of finding out what the relationship of all these factors is in the entire central Amazonian¹ rain forest where the predominant soil type is latosol. Also considered must be the geochemical structure of that region, the division of the area as demonstrated by Fittkau (1969, 1970a, 1970b, 1971a, 1971b; fig. 1), and its influence on the nutrient supply available to the biomass in terrestrial and aquatic environments.

A discussion of the bioenergetics of a tropical rain forest is difficult because few studies have been conducted either on the basis of the specific trophic levels involved or on the basis of the whole biomass. As a consequence, a discussion of available nutrients for specific species at various trophic levels is even more difficult. However, comparisons of litter-fall with the soil complex have been published, and the results are interesting enough to investigate the problem further. In a study by Klinge and Rodrigues (1968), the litter-fall of a central Amazonian tropical lowland rain forest was determined

for 1963 and 1964. The average litter-fall for this period shows that 7.3 metric tons (mt) of dry matter per hectare (h) per year are returned to the soil. Dry matter per hectare is made up of 5.6 mt of leaves, or 76.6 percent of the total dry matter; the remainder is composed of flowers, small fruits, and twigs. It is interesting to note that this amount of litter is smaller than the litter-fall reported for tropical rain forests in Africa and Asia (Bray and Gorham 1964). Klinge and Rodrigues (1968) showed that Amazonian litter is poorer in nutrients when compared with litter from other tropical forests. Results from our chemical analyses indicated that the following raw elements occur in the litter returned to the soil in central Amazonia (kg per hectare per year): 2.2 P, 12.7 K, 5.0 Na, 18.4 Ca, 12.6 Mg, and 105.6 N.

In 1970, estimates were made of the amount of woody material involved in litter-fall of the central Amazonian rain forest (Klinge, unpublished). The results of the analyses show that one mt of stems (stem-part of plant between soil surface and first ramification), two mt of branches (ramifications without leaves), and 1.35 mt of twigs (ramifications bearing leaves), bark, etc. are involved.

Because the 1963-1964 litter-fall experiment was not suitable for the measurement of the total fruit-fall, we calculated roughly the amount of fruits involved in annual litter-fall by kind, weight, and number of fruits in a 2000 m² forest plot. Thus, we determined amounts of 0.35 mt of small fruits (up to 5 g in weight) and 0.5-1.0 mt of larger fruits (over approximately 5 g in weight). We

¹ In this paper, 'central Amazonia' and 'central Amazonian' refer only to the ecological unit of Amazonia defined by Fittkau (1963) and illustrated in figure 1.

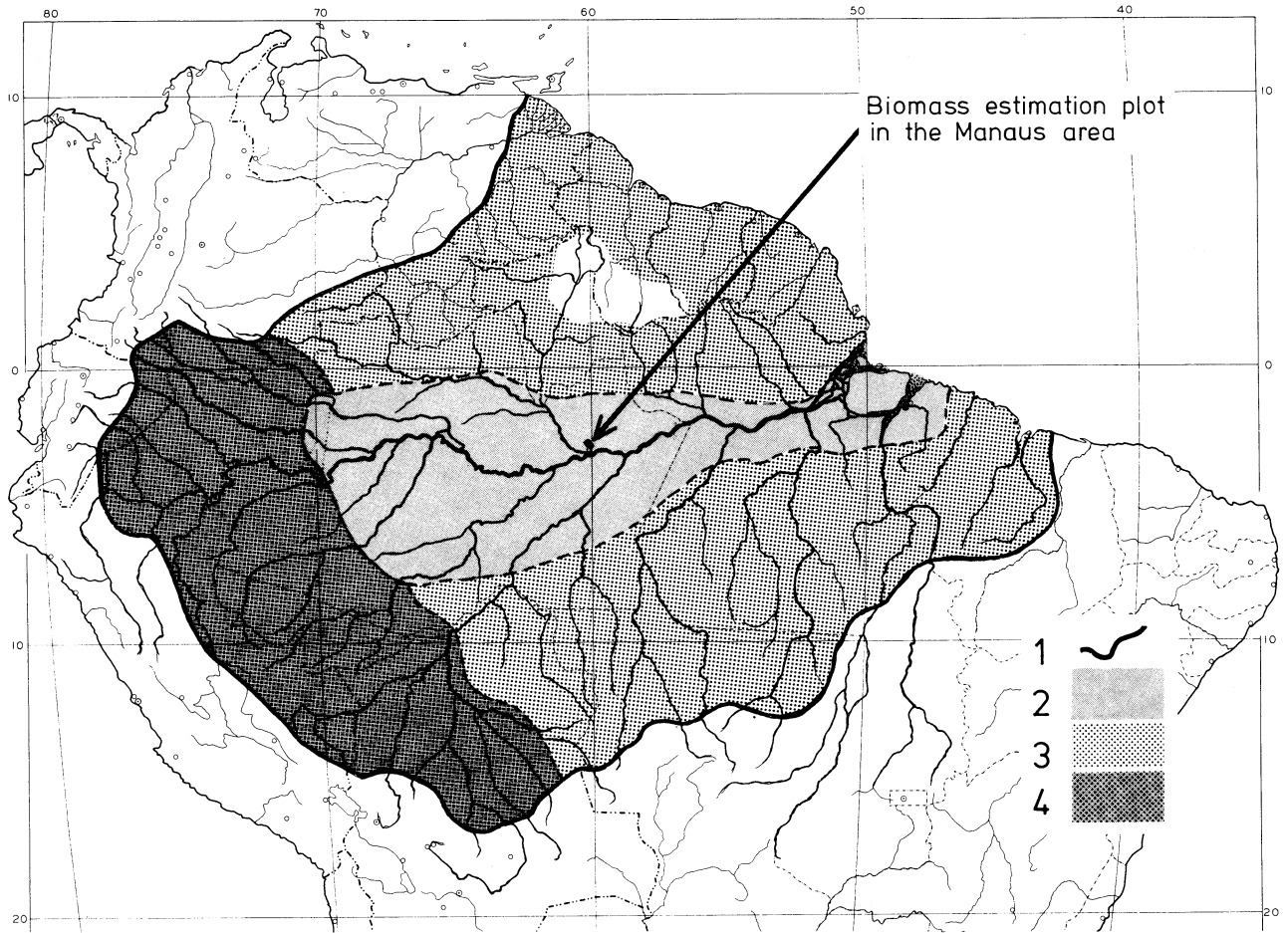


FIGURE 1. Subdivision of Amazonia according to Fittkau (1969). 1—Limit of Amazonian rain forest area. 2—Central Amazonia. 3—Northern and southern peripheral Amazonia. 4—Western peripheral Amazonia.

guess that these amounts are underestimated if we compare our determinations with data for the humid tropical forest on Barro Colorado Island, Panama, as given by Smythe (1970). In a systematic fruit collection experiment, Smythe found about two mt of fruits per hectare per year.

Adding all Amazonian litter fractions, a total of about 11 mt per hectare per year is obtained. This value resembles the litter amount given for a montane rain forest in Puerto Rico which comprises 5.52 mt of small litter-fall, 1.9 mt of log-fall, and 4 mt of brush-fall (Odum 1970). As wood is generally poor in nutrients, the incorporation of so much woody matter in the litter-fall of the central Amazonian rain forest suggests the validity of the above-stated low nutrient content of Amazonian litter.

We also found litter-fall to be seasonal. In the

rainy season of 1964 litter-fall was 400 kg per hectare per month; it was 700 kg per hectare per month in the dry season; the maximum for the dry season, measured in September 1964, was 1000 kg per hectare per month. The seasonality of litter-fall is explained by seasonality of rainfall. About 90 percent of the total annual rainfall of 1771 mm per year at Manaus (Walter and Lieth 1960-1967) occurs during the rainy season which lasts generally from May-June to October-November. However, in 1964 the dry season had begun already much earlier than usual.

In the period from June to November 1970, which was unusually rainy, litter-fall was again measured as was the total litter at the soil surface. The results indicate that litter-fall and litter decomposition were rather well balanced because of the high activity of litter decomposers. According to Stark

TABLE 1. Height classes (meters) and fresh biomass (kilograms) of dicotyledonous trees and palms in central Amazonian rain forest per hectare.

Height class	<0.2	>0.2 - 0.5	>0.5 - 1.0	>1.0 - 1.5	Subtotal <0.2 - 1.5	>1.5 - 5.0
NUMBERS OF INDIVIDUALS						
Trees	} 40,725	} 21,400	} 12,575	} 8,950	} 83,650	6,535
Palms						915
BIOMASS						
Leaves	} 55	91	128	294	513	3,208
Stem		72	200	609	936	2,993
Twigs and branches		1,132				
Total aboveground	55	163	328	903	1,449	7,333
Large roots	25	62	105	247	439	1,542
Fine roots	-	-	-	-	-	-
Total underground	25	62	105	247	439	1,542
Total above and underground	80	225	433	1,150	1,888	8,875
RATIOS						
Aboveground:underground	1:0.5	1:0.4	1:0.3	1:0.3	1:0.3	1:0.2
Leaves:twigs and branches:stem	-	-	-	-	-	1:0.4:0.9
Leaves:wood	-	1:0.8	1:1.6	1:2.1	1:1.8	1:1.3

(1971), decomposition is 5.4 g per m² per day. Klinge (1972a) found a decomposition rate of 0.56 percent per day for leaves, and of 1.5 and 2.3 percent per day for woody litter and fruits, respectively, in the biomass estimation plot.

There is only scattered information regarding the structure of forest which produces the above amounts of litter (Hueck 1966, Lechthaler 1956, Takeuchi 1961). Rodrigues (1967) surveyed a forest and included all trees over 25 cm diameter at breast height (dbh), covering 137,000 hectares in the area of the Manaus-Itacoatiara road. This survey includes the Walter Egler Forest Reserve where the 1963-1964 litter-fall measurements were made. The area studied by Rodrigues also includes a plot which was studied by Klinge and Rodrigues (1971, Klinge 1972a,b,c), for forest biomass estimation. Some results of this recent study are described below.

On a level site at km 64 of the Manaus-Itacoatiara road, a rectangular plot of 2000 m², immediately adjacent the Walter Egler Forest Reserve, was marked off using a nylon line. The plot was subdivided into 40 equal subplots. The area is *terra firma*, i.e., terrain which is never reached by annual river floods. The soil is a yellow latosol of heavy texture (Anonymous 1969). The subsoil is Tertiary sediment (Barreiras Series). The plot was mapped to show the position of all palms and dicotyledonous trees above 1.5 m height and of lianas of more than approximately 5 cm in diameter.

Prior to mapping, all smaller plants were harvested. Total height, stem length, diameter at breast height, and crown diameter of plants above 1.5 m height were measured using a steel tape. Taller plants were measured after felling; smaller plants were measured with a wooden ruler before cutting. In some cases, crown diameters were derived from projections made from the ground.

All leaves, twigs, branches, and stems were separated; leaves by hand, twigs by machete, and branches and stems using a portable chain saw. The fractions were weighed in the field, branches and stems after they were sawed into manageable pieces. Portable balances, weighing up to 100 kg, were used. The root mass of 381 dicotyledonous trees and 51 palms above 1.5 m height was estimated after extraction of the plants by hand or by use of a simple jack. Plants below 1.5 m height were extracted by hand, separated into four height classes and counted, but they were not sampled for taxonomic determinations as in the case of the taller plants. Leaves, shoots, and roots of small plants were also separated and weighed. All fractions of individual dicotyledonous trees and palms of the four height classes under 1.5 m were sampled and weighed, air-dried in the field, and oven-dried in the laboratory at Manaus. All plant parts were finally shipped to Europe for subsequent determinations of nutrients and dry matter. These analyses are still progressing.

The field work extended from mid-June to the

>5.0 - 10.0	>10.0 - 20.0	>20.0 - 25.0	>25.0 - 30.0	>30.0 - 35.0	>35.0 - 38.1	Subtotal 1.5 - 38.1	Total
1,480	725	175	160	55	25	9,155	93,780
45	15	0	0	0	0	975	
1,161	3,253	2,696	3,887	2,277	1,150	17,632	18,145
8,864	37,832	103,241	114,444	126,317	73,410	467,101	467,101
3,193	14,994	53,417	58,419	46,953	21,089	199,197	199,197
13,218	56,079	159,354	176,750	171,547	95,649	683,930	685,379
1,951	6,002	11,952	11,489	10,270	5,356	48,561	49,000
-	-	-	-	-	-	-	206,040
1,951	6,002	11,952	11,489	10,270	5,356	48,561	255,040
15,169	62,081	171,306	188,239	181,817	101,005	732,491	940,419
1:0.2 1:2.8:7.6 1:10.4	1:0.1 1:4.6:11.6 1:16.2	1:0.08 1:19.8:38.3 1:58.1	1:0.07 1:15:29.4 1:44.5	1:0.06 1:20.6:55.5 1:76.1	1:0.06 1:18.3:63.8 1:82.7	1:0.07 1:11.3:26.5 1:37.9	1:0.4 1:11.0:25.7 1:36.8

end of November 1970. During this time many collections were made of large and conspicuous arthropods, amphibians, and reptiles. The vertebrates collected during this time were submitted to Dr. P. Müller, Saarbrücken, Germany, and the invertebrates went to H. Schubart and E. J. Fittkau, Plön, Germany for identification. When evaluating this animal sampling and our observations on animals in central Amazonia made over the last 10 years, we also made use of any information gathered from Indians, settlers, hunters, and professional biologists.

In order to obtain weight data of fauna we listed first those animal taxa (orders, families, etc.) which were observed to have some bearing upon biomass because of their individual weight and/or frequency. Then we estimated density taking into account all observations gathered by ourselves and the above-named sources. Finally, density was converted into weight of the respective group by multiplying weight by density, using average weight of individuals contained in our collections or otherwise determined weight. None of the values thus obtained was adjusted with respect to data found in literature for similar groups in tropical regions elsewhere.

RESULTS AND DISCUSSION

Trees and palms below 1.5 m height were in much greater abundance than taller plants and made up 86 percent of the total plant cover considered (table

1). The number of trees clearly diminishes with height. This relationship is valid particularly for palms which are abundant below 20 m height. The ratios of aboveground biomass, underground biomass, or leaves/branches + twigs/stems, or leaves/wood vary rather consistently from short to tall height classes.

No data are given in table 1 for lianas, epiphytes, and parasites which are represented by the following amounts of fresh biomass: Vascular epiphytes (mainly Araceae, Bromeliaceae, and Orchidaceae), 0.1 mt per hectare; parasites (Loranthaceae), 0.13 mt per hectare; lianas (various families), 46.0 mt per hectare; total 46.23 mt per hectare. Thus we find that lianas are a striking feature of the central Amazonian rain forest, whereas angiosperm epiphytes and parasites are of nearly negligible biomass.

Total weight of the living aboveground biomass of plant origin in the forest is 730.7 mt per hectare. Weight of underground biomass (roots and underground trunks of certain palms) is 255 mt per hectare or 25.9 percent of the total living plant biomass (Klinge, unpublished). Both weights are in agreement with data presented by Rodin and Bazilevic (1964, 1968) and Bazilevic and Rodin (1966). Dead plant biomass at the soil surface (excluding roots) amounts to about 44 mt per hectare of wood and 15 mt per hectare of fine forest detritus, both weights in fresh state. There is, in terms of weight, twice as much stem wood as branch wood.

Total plant biomass of the forest under study is thus about 1100 mt of fresh matter per hectare.

Our herbarium material is actually determined only to the family level. The plant families of which the forest is composed are listed in table 2.

TABLE 2. *Plant families with representatives above 1.5 m height in the central Amazonian rain forest growing on a 2000 m² plot of terra firma latosol.*

Plant family	Numbers of species	Numbers of individuals	Percentage of total individuals
Leguminosae	62	171	8.6
Sapotaceae	43	139	7.0
Lauraceae	40	88	4.4
Chrysobalanaceae ^a	38	96	4.8
Rubiaceae	32	137	6.9
Burseraceae	27	230	11.9
Annonaceae	21	87	4.4
Lecythidaceae	17	132	6.6
Moraceae	17	69	3.5
Palmae	11	196	9.9
Violaceae	10	223	11.2
44 other families	177	409	20.6
Indeterminata	7	9	0.5
Total	502	1986	100.3

^a Refers to the tribe Chrysobalanoideae of Rosaceae but in the familial sense.

If there are in the literature very little data on total plant biomass of humid tropical forests (Greenland and Kowal 1960, Ogawa *et al.* 1961, 1965, Art and Marks 1971, Rodin and Bazilevic 1964, 1968, Bazilevic and Rodin 1966), there is even less information regarding total animal biomass of these forests (Goodnight and Goodnight 1956, Harrison 1962, Hopkins 1967). A rare exception to this lack of information is the study on structure and metabolism of a red mangrove forest in Puerto Rico (Golley *et al.* 1962). There are, however, good descriptions of the fauna living in humid tropical forests, including Amazonian forests (Bates 1965, Dorst 1967, Mann 1968, Mertens 1948), but information on total animal biomass of Amazonian forests is completely lacking. Meggers (1971) states that the majority of wild animals there are small and solitary. Three studies on the central Amazonian soil fauna (Beck 1967, 1970, 1971) do exist, however. Beck, working chiefly in the hinterland of Manaus, studied mainly meso- and macro-soil fauna on sites comparable to our plant biomass study plot. He presented density data for a series of soil animal groups of which only Isoptera and Formicidae are under-represented owing to the technique of collection which he used (table 3).

The overwhelming predominance of Acarina and Collembola, over all other groups, is easily recognized from table 3. Other important groups of fauna are: Isopoda, Pseudoscorpiones, Araneae, Opiliones, Diplopoda (Chilognatha), Chilopoda, Iso-

TABLE 3. *Soil fauna of central Amazonian terra firma rain forest on latosol. Expressed as 10⁶ individuals per hectare; from Beck 1970, 1971.*

10 ⁶ individuals per hectare	Litter	Upper mineral soil	Macro-fauna	Total
Acarina	612	115		727
Collembola	103	16.8	0.34	120
Isopoda	0.7		0.05	0.8
Pseudoscorpiones	2.1		0.09	2.2
Other Arachnida	0.7		0.2	0.9
Diplopoda	2.8		0.1	2.9
Other Myriapoda	3.5		0.03	3.53
Protura	2.8			2.8
Diplura	1.4		0.01	1.41
Larvae of Coleoptera and Diptera	4.0		0.04	4.04
Coleoptera	1.4		0.07	1.5
Isoptera	0.9		0.4	1.3
Formicidae	7.2		1.4	8.6
Aphidina/Coccina	39.4			39.4
Opiliones			0.02	0.02
Blattaria			0.02	0.02
Grylloidea			0.05	0.05
Total individuals	782	144	2.8	929
Biomass (kg)	67.7	12	4.4	84

ptera, Formicidae, Coleoptera and their larvae, and larval Diptera. Moreover, there are regularly present: Scorpiones, Palpigradi, Ricinulei, Uropygi (Schizopeltidia), Symphyla, Pauropoda, Diplopoda (Pselaphognata), Protura, Diplura (Campodeidae and Japygydae), Embiidae, Orthoptera, Phasmida, Forficulidae, Mantodea, Blattaria, Psocoptera, Thysanoptera, Heteroptera, Cicadina, Turbellaria, Hirudineae, Onychophora, Serpentes, Iguanidae, and Dasy-podida.

The lack of any precise information on the population density and biomass of termites and ants, which are so numerous in the environment of central Amazonia, is to be regretted. We may refer only to Beck (1971), who assumed that three quarters of the soil fauna, in terms of biomass, are ants and termites in the central Amazonian rain forest. It is, therefore, not possible to evaluate the role of these soil animal groups in the bioenergy flow within the central Amazonian rain forest. It is impossible to evaluate their role from the literature concerning other tropical regions because of contradicting statements regarding the alimentionation of specific species and population density of different species in different environments. Regarding termites, see Lee and Wood (1971), and Krishna and Weesner (1970). The data given by Wiegert (1970) for *Nasutitermes costalis* (Holmgren) in a Puerto Rican montane rain forest are inappropriate

because of the different type of forest.

The biomass of faunal elements of the central Amazonian rain forest which are important biologically, with respect to production, or because of abundance or size, is given in figure 2. The values have been derived from our general observations over the last 10 years and from observations of others, but not from actual counting and weighing, as stated above. Excepted are: soil fauna, total fresh biomass (84 kg per hectare; Beck 1970, 1971), and certain arthropods and vertebrates which we collected in the biomass estimation plot.

Regarding the zoocoenosis of our forest we found that the following animal groups have a high density: soil fauna (mainly mites and Collembola), Orthoptera (Locustidae, Phasmida), Mantodea, Blattaria, Isoptera, Hemiptera (Heteroptera, Cicadina), and Hymenoptera (Formicidae, Vespoidea). Soil-inhabiting invertebrates are the most conspicuous group comprising the faunal biomass. Below is a detailed discussion of the environment and importance of these soil animals.

The soil contains roots which penetrate more or less one meter into the ground. The main root-bearing zone, however, is only about 30 cm deep. This upper layer contains about half of all fine roots (Klinge 1972c). Because the forest invertebrates listed in figure 2 belong to the soil fauna, and because the soil fauna prefers the uppermost soil layer supplied with organic debris and humified matter, about half the total animal biomass inhabits a zone only 10 cm deep. Thus, in the 40 m vertical range of the ecosystem under discussion, the most important fraction of the zoocoenosis occurs in less than 0.5 percent of the total volume. This fraction of the fauna, however, does not just dwell in this superficial soil layer, but it also feeds on the mostly organic nutrient matter in it.

Regarding alimentation of soil fauna in the tropics, Beck (1970, 1971), in his studies in central Amazonia, and Schaller (1960, 1961), referring to South America and to the tropics in general, stated that tropical soil animals (excluding termites) do not feed so much on organic detritus, as do their counterparts in temperate regions, but also on the fungi which decompose this forest detritus. In explaining this strikingly different feeding behavior between temperate and tropical soil fauna, Beck argues that fungi have optimal growth conditions in the humid tropics where there are constantly high humidity, high temperature, and acidic soil conditions. This argument has also been stated by Eidmann (1942, 1943), Maldague (1958), Maldague and Hilger (1963), and others. Because of these optimal growing conditions for fungi, Beck asserts

further that competition for food between fungi and faunal primary decomposers is much stronger in the tropics than elsewhere. As a consequence of this competition, soil animals are more or less excluded by fungi from the decomposition of organic detritus, and must feed on other material: thus they feed on the fungi themselves. Animal primary decomposers decrease in number, therefore, and secondary decomposers increase accordingly. For secondary decomposers, however, there is not enough organic matter pretreated by primary decomposers. Secondary decomposers also change their food base and change over to feed on fungi. The final result is that fungi become the predominant primary decomposers.

One of the proofs which Beck gives to support his opinion concerns diplopods, which in temperate regions are primary decomposers, while in the central Amazonian rain forest they feed exclusively on fungal mycelia and spores. Regarding other tropical regions, some other authors have reported on fungivorous soil animals. Strickland (1945) referred to fungivorous springtails, beetles, and larval Diptera in Trinidad. Meyer and Maldague (1957) mentioned fungivorous soil animals for the Congo region, Bullock and Khoo (1969) for Malaysia, and Healey (1970) and Coleman (1970) for soil fauna in general.

The surface organic matter or humus of the soil is present as "moder" in the sense of Kubiena (1953), or a "transition between raw humus and mull" (Jacks *et al.* 1966). It is characterized by an absence of mixing of organic and mineral matter, that is, the organic debris layer of moder is separated from the mineral soil below it. The debris layer is well provided with roots and can, therefore, be removed from the mineral soil like a carpet. Moder lacks digging animals or other soil animals which could mix the organic and inorganic components of the soil. There are few Oligochaeta in the central Amazonian rain forest soil and other soil-digging animals are absent (Beck 1971). There are large earthworms (for example, the Glossoscolecidae *Rhinodrilus priollii* Righi), but they do not feed on organic detritus (Beck 1971). These earthworms do not cause active leaf burial, but only incorporate casts among the components of the litter layer. The casts are easily destroyed by rain and are not humic-stained. Madge (1965) observed an earthworm showing similar behavior in a Nigerian rain forest; during the wet season the earthworm, *Hyperiodrilus africanus* (Beddard), produced 36.4 mt of casts per hectare per year. There were 16.4 kg per hectare of earthworms in the soil. In the generally scarce literature on earthworms in tropical rain forest soils

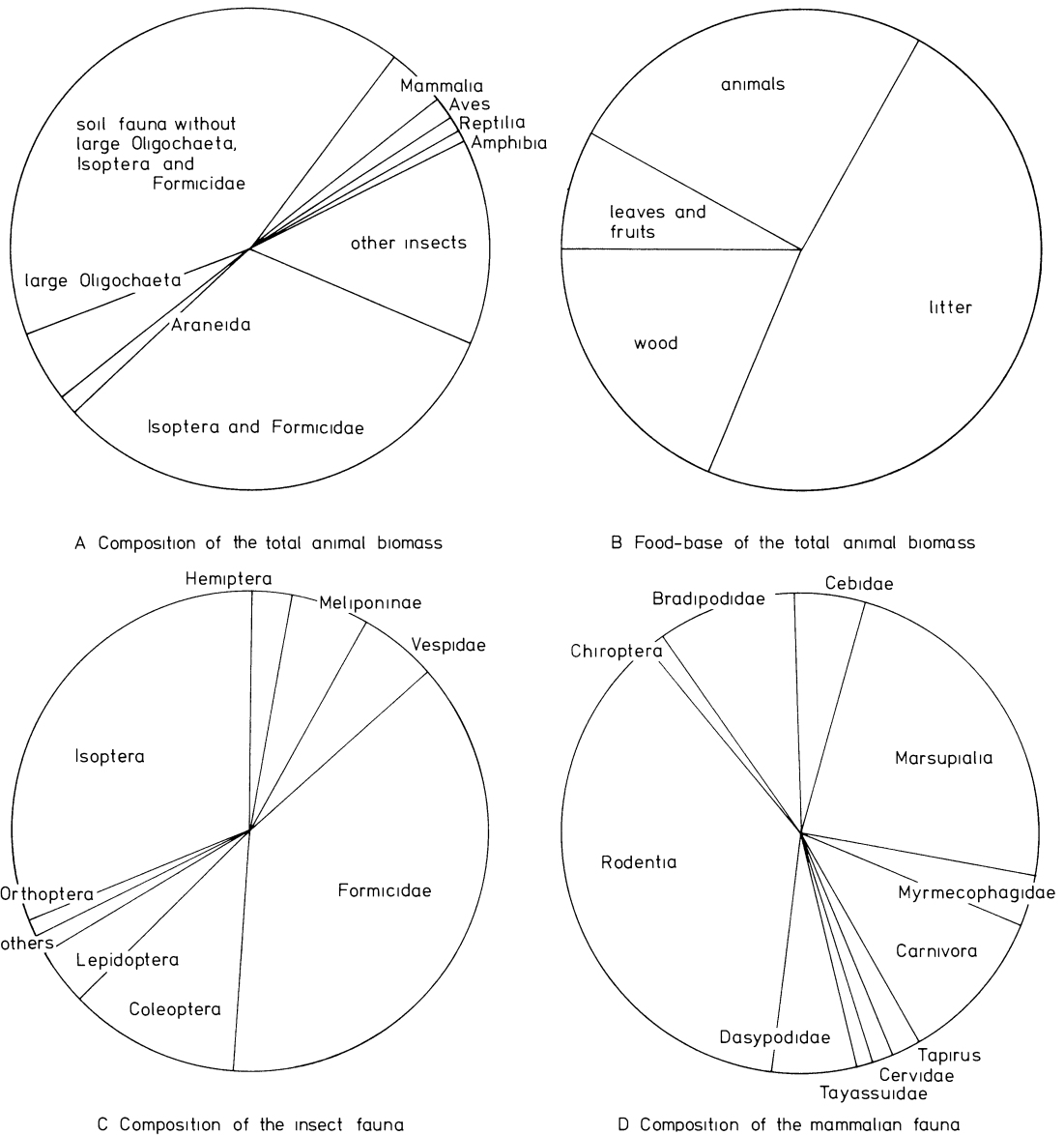


FIGURE 2. Animal biomass, composition and alimentation.

(Bullock and Khoo 1969, Madge 1966, Moore and Burns 1970, Schulze 1967), there is also information on earthworms which feed on leaves of the forest floor (Lyford 1969). Together with *Rhinodrilus priollii*, a large terrestrial leech, *Liostomus* sp., Herpobdellidae, which probably lives on Glossoscolecidae, is found frequently in the Amazonian forest which we examined.

The amount of animal biomass in the central Amazonian rain forest is extremely small when compared with the plant biomass. The poverty in animals is also indicated by the following observations of this forest: Temporary water accumulations in

leaves, palm frond bases, etc. are rarely inhabited by animals. Collecting Amblypygi, even by experienced people, is mostly ineffective (even when a high price is offered for one collected specimen). Collecting insects using light traps is also ineffective. The rarity of rodents can be established from the fact that collections for blood parasite studies by the zoology staff of Instituto Nacional de Pesquisas da Amazônia had to be suspended because of the difficulty of securing the animals. Hunting for human food is never effective (even by experienced people). Food wastes at campsites regularly attract only some Scarabaeidae and Diptera. On faeces,

only some Diptera may be found. In the biomass estimation plot, one uninhabited wasp nest and one small bee nest were found. Only one Aviculariidae was collected there, and butterflies were seldom observed. Only termites and ants are frequent, judging by the number of their nests in the earth, on the soil surface, and attached to tree trunks and branches, and by the trouble they cause to humans working in the forest. Curculionidae and Cerambycidae are also relatively frequent.

The small percentage of animal biomass compared with the total biomass of the central Amazonian rain forest becomes much more evident if we compare similar figures for African steppes and savannas, or for other tropical forests. In a montane tropical rain forest in Puerto Rico, the animal biomass comprises 0.1 percent of the total biomass (Odum 1970, Odum and Pigeon 1970, Odum *et al.* 1970), while in central Amazonia it comprises only 0.02 percent of the total biomass. In Tanganyika and Uganda grasslands there are 100-300 kg per hectare of large herbivorous animals (Wiegert and Evans 1967). In the East African savanna are 235.6 kg per hectare of these animals, and in Ghana forests there are 0.72 kg per hectare of ungulates and primates (Bourlière 1963). In an East African thornbush savanna, having a dry matter production of 1-7 mt per hectare per year, on each hectare there are 50 kg of ungulates, 4 kg of plant-eating small mammals, and 250 kg of plant-consuming soil animals which feed on the dry matter produced each year. Also present on each hectare are 0.3 kg carnivores (Hendrichs 1970).

It is remarkable that the main part of the animal biomass of the central Amazonian rain forest is present in that part of the ecosystem which is well supplied with forest debris and in which the debris is processed. Correspondingly, the proportion of the animal biomass feeding on living plant matter is rather small. The enormous proportion of wood in the living plant biomass contributes little to the food resources of the fauna. Beetles and their larvae, and termites, are the most important faunal elements feeding on wood. Termites are supposed to be the most effective wood-eaters, but, as stated above, no precise information is available regarding energy and matter flow through this animal group in central Amazonia.

The leaves, which comprise about 2 percent of the living plant biomass of our forest, are utilized by a relatively small number of taxa and individuals (Orthoptera, *Atta*, Coleoptera, Hemiptera, Lepidoptera, sloths, and parrots; primates also consume young leaves, leaf buds, and flowers). Leaf-cutting ants are mostly responsible for the defoliation of small trees

which occur here and there in the forest.

Damage attributable to insect plagues was never observed nor reported (Voute 1945-1946, Schneider 1939). The opinion that a great proportion of the leaves of tropical rain forest plants is consumed by animals before they fall on the soil appears to us to be rather exaggerated and seems not to be generally valid for all tropical forests. Inspection of living leaves in the course of leaf harvest as part of the biomass estimation, as well as of leaves lying on the soil, never showed any signs of heavy attack by animals. Our observations agree with the statement of Madge (1969) who, in a study of litter decomposition in Nigeria, expressed the view that primary food consumption of leaf litter appears to be less in the tropics than in temperate regions. His opinion is also supported by Wanner (1970) who wrote: ". . . direct grazing seems to be a minor pathway of energy flow in rain forest as elsewhere."

There is some controversy in the literature regarding leaves consumed by tropical rain forest animals. The most extreme position is held by Eidmann (1942, 1943) and Büchler (according to Mann 1968) who reported that 25 percent of the leaf matter is consumed by insects in West African and South American forests. Hopkins (1967) estimated that 67 percent of the primary production in a Nigerian rain forest travels along the grazing pathway. Bray (1964), however, estimated the loss of leaf matter due to herbivorous grazing to be 1.5-2.5 percent of the annual leaf production. Odum and Ruiz-Reyes (1970) estimated that 7 percent of the leaf area is consumed by animals of the Puerto Rican Tabonuco rain forest. Cruz Acosta (1964) stated that less than 6 percent of leaf matter was consumed by insects in a Costa Rican rain forest. Chrysomelids and butterfly larvae are mainly responsible for the consumption of living leaves in a West African rain forest (Eidmann 1942). Butterfly larvae were only occasionally observed, and in small numbers, in the central Amazonian rain forest near Manaus.

Cruz Acosta (1964) agrees with Bray (1964) that leaf utilization by animals is correlated with the nutrient content of the leaves. We assume that our finding of a relatively low nutrient content in central Amazonian leaf litter supports this view (Klinge and Rodrigues 1968). Also it has been frequently observed in Amazonia that where fresh mineral soil has been recently dug and exposed to the air, and especially if it is polluted by urine, butterflies, bees, and other insects can be found in large numbers visiting this matter, presumably in search of nutrients. A heavily perspiring man is strongly at-

tacked by Meliponinae which suck up the sweat; this circumstance is especially true in the highly oligotrophic Rio Negro area. Both observations seem to us to be an indication of the shortage of nutrients in Amazonia. The physico-mechanical properties and organic composition of leaves will also play a role in making the leaves either attractive or unattractive to animals.

At any given time, fruits and flowers are only present to a small degree (Bourlière 1972) because of the low species density of plants (table 2). These plant organs, therefore, represent only a small food base and do not serve as a continuous source of nutrients for a very important part of the fauna. Meggers (1971) also adheres to our opinion regarding Amazonian *terra firma* forests and points out that in this region the distribution of individuals of the same plant species is scattered so that ripe fruits or seeds are not available in concentrated numbers. She included aboriginal man in her thesis and stated that he, subsisting on wild animals and plants, affected the ecosystem in a way similar to other kinds of large animals.

In the past, reference has been made to a "fauna of tree crowns" in tropical rain forests, thus indicating a specific environment in that part of the ecosystem. Our observations agree with the findings of Harrison (1965) regarding vertebrates in Borneo and contradict the assertion that life in the crowns of trees is highly significant. We have observed certain kinds of adaptations of fauna to a life in the crown area and on bark; for example, protective or cryptic coloration of locusts, mantids, cicadas, beetles, and reptiles. On the other hand, our opinion is that the fungi which inhabit the soil are the main primary decomposers and are highly significant in processing the forest litter and in concentrating the low levels of nutrients stored in the dead organic matter. It is nevertheless true that large amounts of plant matter are produced in the tree crown zone of the forest. But the conversion of the bulk of plant matter to living animal matter must pass through the bottleneck of the dead plant matter which accumulates in the litter layer of the forest soil. This zone is inhabited by soil fungi which can incorporate nutrients of the forest detritus into their mycelia, thus concentrating the limited nutrients and making them available for organisms at the next higher level of the energy pathway.

The critical point in the energy and nutrient transformation is the inability of soil invertebrates to process large quantities of dead plant matter into living matter in strong competition with fungi as described above. Exceptions to this pattern are found in taxa having representatives of microorgan-

isms in their digestive tract, as in ruminants, the tropical termites, and other insects living in symbiosis with microorganisms. These animals can digest large quantities of food, such as wood, to obtain a minimal nutrient level for their existence.

Our contention that the main energy flow is undoubtedly through the detritus food chain (fig. 3) is strongly supported by Cruz Acosta (1964) and by Went and Stark (1968). When studying the biological role of soil fungi in the Amazon rain forest, Went and Stark proposed first a very intensive fungal development, some fraction of which is in the form of mycorrhiza. Then they argue that fungi are the primary decomposers of the forest litter and thus agree with the conclusions of Beck (1970, 1971). Went and Stark further assert that the nutrients liberated during the decomposition of forest litter by fungi are not released into the soil but are transferred to the tree roots through mycorrhizal fungi which are restricted to the surface organic layers of the soil. They believe that the same fungal mycelium acts as primary decomposer and as mycorrhizal mycelium.

The dependence of the lower members of the consumer chain on organic detritus and on microorganisms feeding on it in the terrestrial environment has its parallel in the aquatic environment of central Amazonia in which no primary production has been observed as yet. There is a striking number of such groups of aquatic animals which feed on organic micro-drift and on "detritus" (Fittkau 1967, 1970b, Sattler 1963, 1967).

In conclusion, we believe that in the tropical rain forest of central Amazonia dead organic matter is processed by microorganisms which channel organic matter and nutrients through their own matter into the consumer chain. This type of forest occupies the vast level plain built up by Tertiary sediments (Barreiras Series) of the *terra firma* which is never reached by the annual floods of the drainage ways. The hinterland of Manaus where we conducted our studies forms part of central Amazonia and lies between the Rio Negro and the Rio Solimões. It is clearly to be distinguished from the sandy Rio Negro basin, despite the fact that small sand patches are spread throughout central Amazonia. The rain forest of the central Amazonian *terra firma* is characterized by a very high number of dicotyledonous trees and by a great proportion of palms and lianas. Small, slender trees predominate. Total plant biomass of the forest is about 1100 mt of fresh matter per hectare while its animal biomass is only 0.2 mt per hectare. Invertebrates predominate. Insects are well represented. Soil fauna, comprising approximately 50-75 percent of the animal

biomass, is the most important group from the points of view of ecology and energy flow. Living plant matter apparently does not serve as the main

food base of animals. Seven percent of the animal biomass feeds on living plant matter, except wood, and 19 percent feeds on living and dead wood.

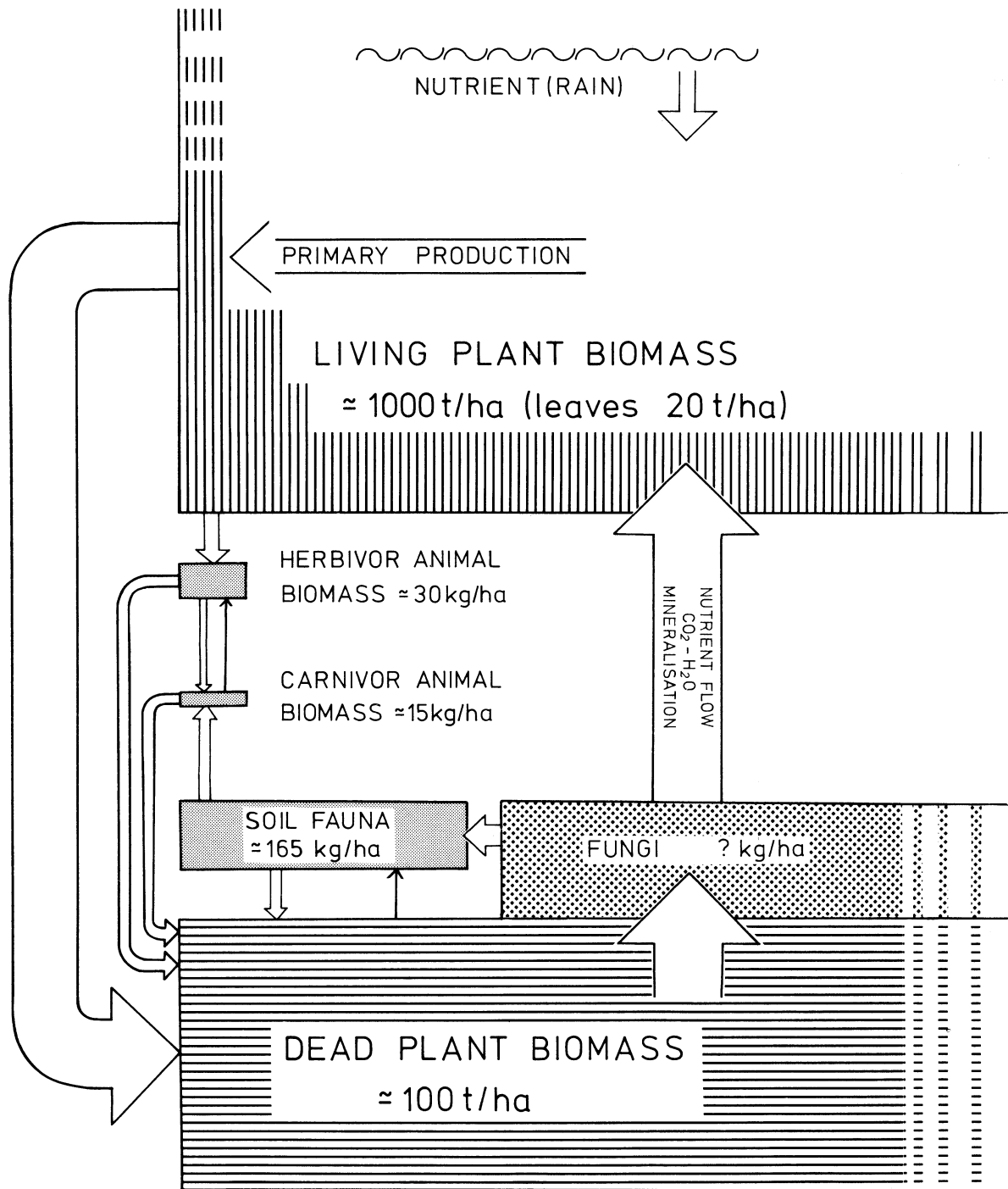


FIGURE 3. Schematic distribution of biomass and organic matter flow in the central Amazonian rain forest ecosystem.

About half the animal biomass feeds on litter, mainly after it is converted into fungal mycelia.

The food chain is thus built up on transformed litter. Twenty-four percent of the animal biomass is carnivorous and about 2 percent is omnivorous. The preferred utilization of transformed dead matter is believed to be connected with the small nutrient supply of living plant matter and with the ecosystem as a whole. The food chain in the waters of the region supports this thesis (Fittkau 1973).

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