drained soil of the terra-firme forest is largely dependent on the following two factors: 1) the declivity which determines lateral drainage of the soil, 2) the forest architecture which conditions the intensity of the light that is received by understory plants. However, the two factors are mutually dependent. Local topography not only determines declivity, but also interferes with the pattern of forest architecture. It plays an immediate role in the modification of drainage and thus of water supply, and affects forest architecture by influencing the frequency of tree falls.

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Litter production and decomposition in a terra-firme forest of Central Amazonia

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Summary. Chemical and biological aspects of litter production and decomposition were studied in three distinct areas of the Central Amazon. Litter production was measured during three years, employing the litter trap technique, with adapted conical collectors. Leaf litter decomposition was studied in experiments over five-month-periods with repetitions for the dry and wet seasons, using the nylon-mesh bag technique. The greatest litter production took place during the drier period of the year, mainly from June to October, while decomposition processes were more accentuated in the wet season: in the plateau site, one-half of the litter disappears, according to a mathematical model, in about 218 days under dry season conditions as against 32 days in the wet season. In the rainy season, weight reduction and mineral losses from decomposing leaves occurred more rapidly, owing to the intense biological activity on the material during this period. Particularly noticeable was the intense activity of termites in organic matter breakdown and mineral removal, and the extensive root penetration in the decomposing leaves, which removed some minerals but increased the amounts of others. Leaching effects were also quite noticeable in this period. During the rainy season, in the latosol sites, termites were responsible for more than 40% of the removal of decomposing leaves. While intense biological activity appears to be the major factor responsible for weight reduction and loss of many minerals, as well as for the accumulation of some other minerals (mainly zinc, iron and aluminium) in the decomposing material, leaching seems to be the major factor responsible for the loss of certain minerals such as potassium, boron and copper.
Key words. Litter; litter decomposition; nutrients cycle.

Introduction

Organic material represents a component of vital importance for the majority of the functional processes occurring in the soil of forest ecosystems[16]. The greatest contribution to the soil humus layer is litter, that is the detritus falling from the forest onto the soil surface.

Litter plays a fundamental role in the cycling of nutrients and in the transfer of energy between plants and soil[31], functioning as a fuel source for the nutrient cycles in the uppermost layers of the soil. It is particularly important in the nutrient budgets of forest ecosystems on nutrient-poor soils, where the vegetation depends in large part on the recycling of the nutrients contained in the plant detritus[38].

In spite of this, there have been very few studies of the dynamics of surface nutrients in forest soils[16]. This is due to the complexities involved and the fact that the majority of studies to date refer only to litter production and chemical content, without considering its transformation into soil and plant nutrients. Only in recent years has there been an increase in the number of studies dealing with the dynamics of dead material in forest ecosystems, although the majority deal with temperate and/or homogeneous forests. With reference to tropical forests, the recent studies in the Pasoh forest, Malaysia[24], in Central America[11,15], and in Venezuela, principally by the San Carlos do Rio Negro Project[18,21-23,39,40], have taken into account the dynamics of mineral nutrients in natural forest ecosystems as well as those cut and burnt by man. Very few studies of this nature have been carried out in the Brazilian Amazon. The most important are those of Klinge and Rodrigues[28], Franken et al.[14], Silva[36], and Silva and Lobo[37] concerning litter and its chemical content, Klinge[25-27] on litter production and decomposition, and Irmler and Furch[20] on litter decomposition and nutrient release in the dry phase of inundated forests. The project 'Bacia Modelo' was started in 1976 in an intact hydrographic basin, approximately 80 km north of Manaus, with the object of studying the entire functioning of a humid Amazonian terra-firme tropical forest ecosystem.

This included studies of the production, decomposition and liberation of nutrients from litter (Luizão and Schubart, in preparation) and the growth of fine root systems in decomposing material[33]. The majority of the findings that we will present and discuss have arisen from the studies carried out in the 'Bacia Modelo' project of the National Institute for Amazon Research (INPA) and specifically from the master's thesis of the first author[30] which studied biological aspects related to decomposition, such as the rate of liberation or disappearance of litter mineral nutrients in two primary forest areas and 3-year-old second growth forest, comparing both dry and wet seasons. Of the two primary forest areas, one (area A) was a plateau of yellow clay latosol and the other (area B) was a hydromorphic podzol stream valley bottom. Both soil types are common in the Amazon basin and are generally very poor in nutrients[5,35] in spite of the exuberant forest cover of large biomass and a high species diversity[17,32]. The 3-year-old second growth forest (area C) was also on a yellow clay latosol[9], similar to that of area A. The area had been deforested manually, burnt and used for a single subsistence crop. At the beginning of the study, the vegetation was approximately 8 m high with a predominance of the genus *Cecropia*. The approximate geographic coordinates of the 'Bacia Modelo' study site are: Lat. 02°34'S, Long. 60°07'W.

Litter production

The litter produced by the vegetation in each area was collected in 15 conical traps (80 cm in diameter, 1 m high), the contents of which were removed each week so as to minimize decomposition effects. The plant detritus was dried, separated into leaves and other components (grouped), weighed and kept for later chemical analyses. In the three years of the study, the highest litter production was obtained for the primary forest on the plateau, and the lowest for the young second growth. Total litter production and the percentage of leaves in relation to total litter weight during the first year of the study (1979–1980) are shown in table 1. It can be seen that a large part of the litter produced is represented by leaves, especially in the young second growth, which is characterized by accelerated growth rates requiring a large leaf biomass which is rapidly replaced.

These results, although similar to those for other tropical forests, indicate much lower rates of litter production than frequently cited world means[34].

With reference to the variation in litter production during the year, there is a notably greater production in the driest periods, especially from June to October. This is especially so for the plateau forest which has the highest peaks in August and September, the driest months of the year. The forest of the stream valley bottom, although exhibiting relatively high production in the dry period,

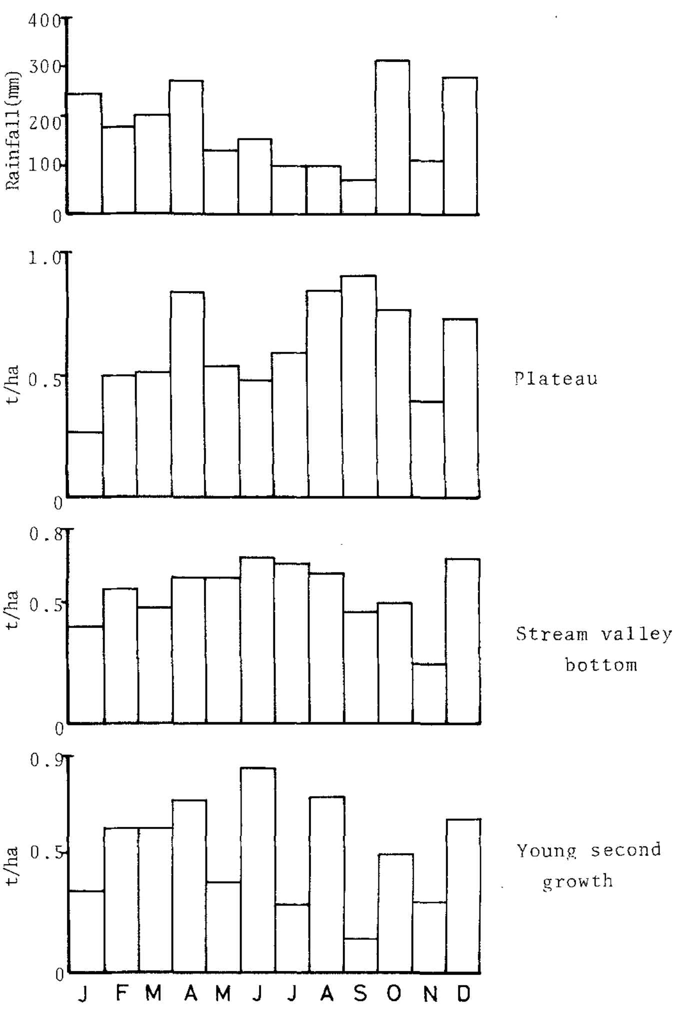

Figure 1. Monthly litter production (dry weight of material in t/ha) during the year in the three study sites. Also shown is the total rainfall (mm) for the corresponding months.

Table 1. Annual litter production (t/ha·y, dry matter) in the three study sites ( ) = standard deviation; N = 15

Area	Total litter	Leaves only	% of leaves in relation to total litter
A Plateau	7.42 (2.128)	4.41	59.5
B Stream valley bottom	6.48 (1.625)	4.05	62.5
C Young second growth	6.07 (2.927)	5.17	85.2

shows little variation in detritus fall. Litter production in the young second growth shows great irregularity (fig. 1). Secondary peaks in detritus production can be seen in the months of April and December in all areas. Although these periods were during the rainy season, these two months followed others with little or less rainfall.
However, no direct correlation was found between precipitation and detritus fall in each month nor for the previous or following months. This can only be verified with data collected on a weekly basis.
Other studies carried out in the regions of Manaus[14] and Belém[27] showed a higher plant detritus production (7.8–8.0 and 9.9 t/ha, respectively) as well as a higher percentages of leaves (between 70 and 80% of total litter).

Mineral nutrient transfer

Although the quantities of litter produced are less than those for many other forests and have relatively low nutrient values[19], the quantities of nutrients that arrive on the forest floor from the litter are considerable, relative to those already present in the soil. The quantity of nutrient stored in the biomass is very large compared to the stocks in soil. An idea of this is gained from table 2 which shows the transfer of mineral nutrients from the vegetation to the soil by means of detritus fall in relation to the total quantities already stored in the soil and the vegetation. The percentage values for nutrient transfer shown here are relatively low because they are percentages of the *total* amounts of nutrients in the soil and vegetation rather than the amounts of *exchangeable* nutrients. The amounts of available nutrients are considerably smaller. Data obtained by Chauvel[8] show the following values for the total amounts of bases (in ppm – parts per million) for the horizon AB (between 15 and 30 cm depth): Ca = 920, Mg = 182, K < 78, Na = 805 and Total = 2005, while the exchangeable quantities for bases were only 12, 3.6, 7.8, 4.6 and 28, respectively.
Besides the nutrients transferred from the vegetation to the soil by means of leaf and fine detritus fall, there is a certain input of nutrients into the soil from slowly decomposing dead tree trunks, as well as throughfall.

Table 2. Mineral nutrient transfer from the vegetation to the soil by means of leaf and fine detritus fall[28] in relation to the total amounts of these nutrients in the soil and in aerial parts of the vegetation of terra-firme forest near Manaus[25]

	P	K	Ca	Mg	Na
Soil to 1 m depth (kg/ha)	147	58	0	23	50
Vegetation (kg/ha)	59	434	424	202	193
Transfer vegetation-soil (kg/ha/y)	2.2	12.7	18.4	12.6	5.0
% in relation to soil	1.5	21.9	–	54.8	10.0
% in relation to vegetation	3.7	2.9	4.3	6.2	2.6

Litter decomposition

The decomposition of litter (in its broadest sense, including leaching, disintegration, removal, and mineralization) was studied using the method of nylon mesh bags[2]. Leaves from only one species were used to permit a comparative study of the decomposition rates and mineral nutrient dynamics in different environments and seasons, thus avoiding the difficulty imposed by the diversity of leaf species typical of tropical humid forests. Sixty nylon bags of 1 mm mesh, measuring 20 × 24 cm, were placed in each study area. The bags also had lateral perforations of 9–10 mm to permit the entry of soil macrofauna. Each bag contained approximately 20 leaves of *Clitoria racemosa* Benth. (Leguminoseae) of known weight and chemical content. They were placed in the leaf litter layer, in sites cleared of other recently fallen leaves. Ten bags were removed at regular intervals (after 15, 30, 60, 90, 120 and 150 days). The experiment was carried out once in the wet season and once in the dry season. The bags removed after each interval were examined for biological activity and then dried, weighed, fragmented and analyzed to determine mineral content. By this means weight loss and changes in mineral content were determined at various stages of the decomposition process. Knowing the initial mineral content we could determine the percentage loss (or in some cases increase) of each constituent analyzed. Thirteen components were analyzed: N, P, K, Ca, Mg, S, (macroelements, results as percentages), Fe, Cu, Mn, Zn, B, Na, and Al (microelements, results in parts per million – ppm). The analyses were done in the laboratories of the Centro de Energia Nuclear na Agricultura (CENA), Piracicaba, São Paulo.
The leaf weight loss was greater and faster in the wet season for all three study sites (fig. 2). The greatest leaf weight loss was recorded for the young second growth (area C) during the wet season. In the dry season this was true of the plateau forest (area A). The lowest weight losses were recorded from the stream valley bottom in both wet and dry seasons.
By means of an adjustment of a double exponential model[7,44], we calculated, using an iterative method, the times in which the material is reduced to a half and to 5% of its initial weight (table 3).
The large difference observed between the dry and rainy seasons, with a considerable acceleration of the decomposition processes in the latter, is apparently not directly dependent on precipitation. There is only a weak statistical correlation between the percentage weight loss and the rainfall total in each month. The effect is largely indirect in that the humidity conditions typical of the rainy season favor an increase in the activity of both micro-decomposers and macro-arthropods, which remove the litter. The latter appear to be most affected by adverse humidity conditions during the dry season[1,13,41]. Besides this, the increased humidity stimulates the growth of fine surface roots which penetrate the decomposing material[33].
The greater penetration of fine roots and, principally, the intense activity of the macro-arthropods removing the organic material, appear to be the factors which determine the enormous difference in litter weight loss between the dry and wet seasons. Direct observation of the biological activity in the samples, which showed close

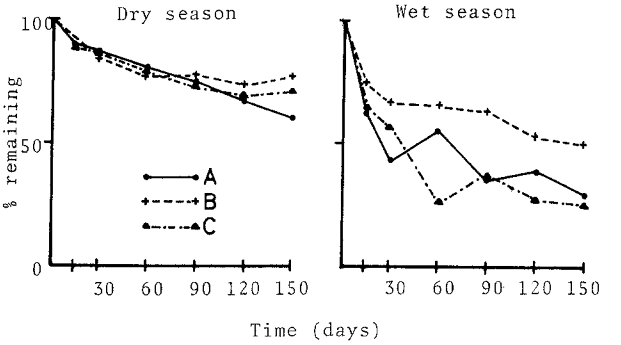

Figure 2. The dry weights of the material remaining after each stage of the decomposition process in relation to initial dry weight. (A) Plateau; (B) Stream valley bottom; (C) Young second growth.

agreement with that predicted by the double exponential model, indicates the very important role of macro-arthropods, especially of termites of the genus *Syntermes*, which remove considerable quantities of litter from the surface to the deeper soil horizons. For the latosol sites, we calculate a litter weight loss increment of 40% or more during the wet season, due to termite activity alone. This estimation is confirmed by indices obtained from the adjusted curves of the double exponential model (Schubart and Luizão, in prep.). Termites in this region are considered one of the largest groups of the soil fauna, the other being ants, and the most important with regard to decomposition processes[12]. Leaf litter weight loss is therefore directly related to termite activity, which can also degrade such resistent substances as lignin[4]. The abundance of large *Syntermes* termites, which cut little round discs from the leaves and carry them to their underground galleries, indicates that they are largely responsible for the transportation and concentration of organic material observed in the soil profiles of Central Amazonia (A. Chauvel, pers. comm.).

Fine roots, which penetrate the nylon bags and interlace with the leaves, are effective components of the decomposition process. By exudation, direct absorption or transfer by mycorrhizae, the roots remove a number of essential nutrients from the decomposing material[18,42,43]. Recent research in Venezuela has shown that fine root penetration can accelerate the rate of decomposition of litter in mesh bags by as much as 50% (E. Medina, pers. comm.) In our study, root penetration was much greater in the wet season and in the clay soil sites, principally the primary forest where surface roots are more abundant. In this region it has been estimated that the surface to 10 cm depth contains 84.8% of all the roots of diameter less than 2 mm and 65.9% of all roots with diameter between two and 10 mm (Chauvel, Guillaumet and Schubart, unpubl.) and that both root growth and root productivity above the soil are appreciably greater in the wet season[33]. In the final stages of the decomposition experiment, the volume of roots in the nylon bags was sometimes greater than that of the remaining leaves, although their weight was generally much less.

As for other observed biological activities related to leaf decomposition, worms were relatively rare in the study sites, indicating a lesser role in the decomposition process; enchytraeids (potworms) were also uncommon and their participation was very limited. The micro-arthropods and microorganisms certainly play a much more important role: in the dry season when macro-arthropod activity was reduced and the amount of root penetration was very small, a large part of the weight loss, although slow, must be credited to them. Although their role is intensified in the wet season, their effect is masked by that of the macro-arthropods.

Leaching, principally by rain, is another factor determining the rate of litter decomposition. It is more important in the initial stages and, of course, during the rainy season. However, it is not the major factor responsible for loss of mineral constituents, as will be discussed in the next section.

Table 3. Time (days) in which the material is reduced to 50% and 5% of its initial weight in the three study sites

		T_{50}	T_{95}
Plateau	Dry season	218	1006
	Wet season	32	702
Valley	Dry season	3332	22008
	Wet season	157	1076
Second growth	Dry season	466	2756
	Wet season	30	1208

Dynamics of litter mineral nutrients

Chemical analyses of the leaves used in the decomposition experiment, both before and after various periods of exposure, enabled us to follow changes in the mineral content of the litter during the five months of each trial. We also attempted to identify the principal mechanisms by which mineral constituents were lost from the leaves. The following results refer only to the plateau forest (area A).

Some mineral constituents such as potassium, boron, and in the rainy season, copper and sodium, were evidently highly subject to leaching; disappearing or attaining minimal levels in a very short time. Of these, potassium and boron are the most typical examples of leaching effects on litter[3,16] in spite of indications of some biological absorption (roots penetrating the material).

Other constituents, such as phosphorus (fig. 3) and magnesium (fig. 4), behave in such a way as to indicate that part of their removal results from leaching but the remainder most clearly from biological action (absorption by roots and associated mycorrhizae and the activities of microorganisms and arthropods). These elements

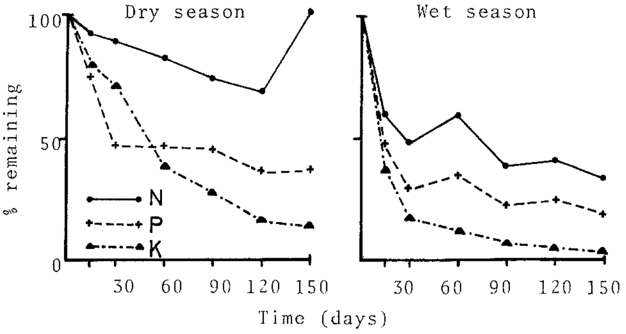

Figure 3. Levels of nitrogen, phosphorus, and potassium remaining in the decomposing leaves. Plateau forest.

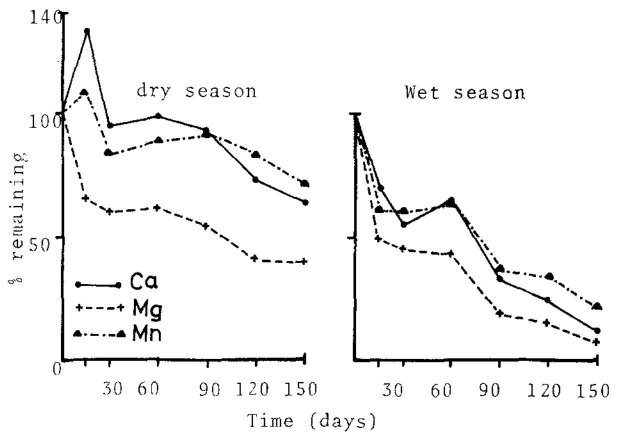

Figure 4. Levels of Calcium, magnesium, and manganese remaining in the decomposing leaves. Plateau forest.

disappear from the decomposing material at a considerably faster rate than would be excepted by weight loss, as has been shown by other authors[3,29]. In the rainy season, the loss of these elements was rapid initially but later slow and gradual, until it reached very low levels in the leaves. The levels of nitrogen (fig. 3) and of sulphur showed considerable oscillations, especially in the dry season when they displayed a marked increase in the final stages of the trial. This increase, demonstrated in experiments by other authors, results from a general concentration of organic compounds produced, liberated and/or excreted by the microdecomposers acting on the material[10,16]. In the rainy season, there is marked nitrogen and sulphur loss, especially in the early stages of decomposition, which almost accompanies the weight loss curve of the total organic material (fig. 2). This indicates a joint action of leaching processes and the intense action of the decomposers removing the nutrients.

In the dry season, calcium and manganese contents show a slight initial increase followed by a slow and irregular loss after 30 days. In the wet season losses were more accentuated, and towards the end of the trial exceeded the total weight loss. The initial increase of calcium and manganese in the dry season is explicable by the fact that these are elements of the leaf structure, and are affected little or not at all by the initial leaching and attack by microdecomposers, processes which predominate during that time of year. As a result of this there is a general increase of these elements in the decomposing material. In the wet season, however, this increase does not occur because of the greater activity of macrodecomposers, especially *Syntermes* termites which remove discs of both the lamina and veins. Calcium and manganese are removed along with the organic material and evidently also suffer leaching effects in the final stages of decomposition. Besides this, there are indications that the roots penetrating the organic material also absorb small quantities of these elements, especially during the wet season.

Zinc, iron and aluminium (fig. 5) are the elements which present the greatest accumulations in the decomposing material, especially in the dry season. The very high increases in these elements, especially of iron and aluminium, result not only from the fact that they are accumulated in the parts of the leaves which are the least subject to decomposition because they are parts of the leaf's structural elements, but also as a result of the activities of the decomposers, besides the washing of the aerial phytomass by rainwater and the roots which penetrate the leaves. The roots of higher plants could, for example, be accumulating aluminium to avoid its toxicity[10] and then be depositing it on leaves. Zinc and iron might also be transported from the soil and plants to the material by way of the fine roots. Part of the rainwater reaches the litter layer after washing the aerial phytomass. On evaporation, most rapid during the dry season, it leaves quantities of zinc, iron, aluminum and other elements on the leaves. However, the greatest contribution to the increase in levels of these elements is, undoubtedly, through the action of the decomposers, especially the macroarthropods which, on attacking or visiting the material, carry with them considerable quantities of soil residues which are rich in these elements, especially iron and aluminum[8].

In the dry season leaching is reduced which results in a greater concentration of these constituents in the region's soil surface[6] which compensates for the reduced arthropod activity at this time. In this way, the accumulation of soil residues on the leaf surfaces is able to provoke a considerable increase in the amounts of zinc, iron and aluminum, which appear in levels ten or twenty times greater in the isolated residues than in the decomposing leaves (Luizão and Schubart, in prep.).

The transport of soil residues rich in iron, aluminum and zinc, together with a relative increase of the elements of the leaf structure such as calcium, manganese, and zinc, and the deposition of metabolic products or excreta of the microorganisms and soil fauna which cause accumulations of nitrogen and sulphur, result in a net increase of the 13 mineral constituents analyzed, most especially in the dry season (fig. 6).

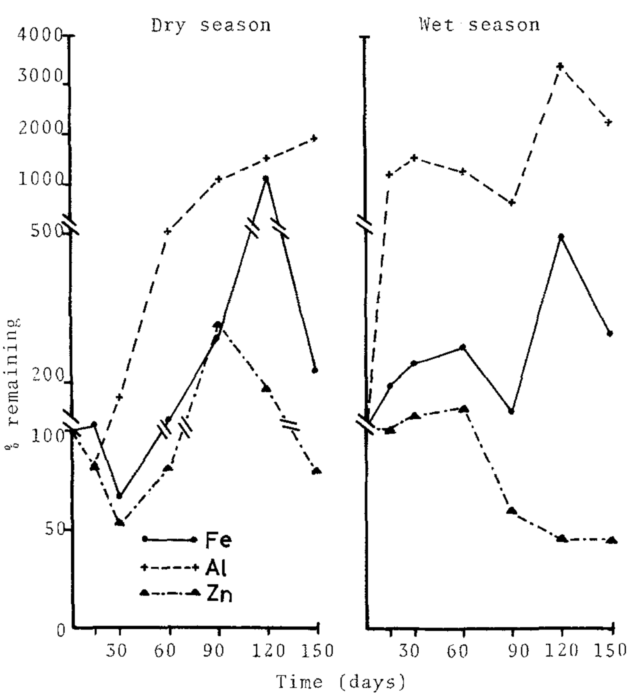

Figure 5. Iron, aluminium, and zinc levels in decomposing leaves after each stage of the decomposition process in relation to initial content. Plateau forest.

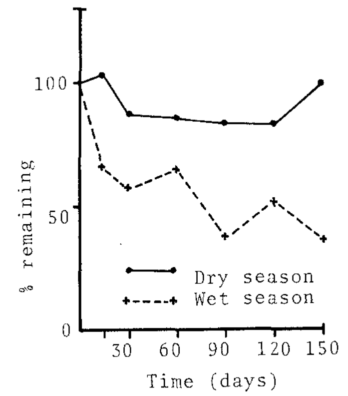

Figure 6. Summed levels of the 13 mineral constituents in the decomposing material. Plateau forest.

The increases are enough to produce a net increase in the remaining material equal to or greater than the initial contents. This clearly indicates that there is a real accumulation of some mineral elements from the immediate surroundings onto the decomposing material of the litter layer.

In general, taking into account the summed totals of the mineral constituents at the beginning of each trial and at the various stages of decomposition, it is possible to observe a considerable difference between the dry and wet seasons. In the dry season, after an initial decrease due to the leaching of the most soluble elements and the breakdown of carbon compounds, there is a clear increase in the total content of the mineral constituents of the decomposing material. In the wet season there is a considerable diminution of the constituent minerals, closely accompanying the weight loss of the leaves; that is, accompanying the disappearance of organic material. Initially, weight loss is very rapid, but it later becomes slower and more gradual, although total losses are consistently less than the weight loss, indicating that accumulations in the rainy season are still considerable for some mineral constituents, as is the case for iron and aluminum.

Final considerations

As there is greater litter production during the driest periods of the year when decomposition processes are slowest there is a general deepening of the leaf litter layer, which is reversed during the wet season. For this reason, it is during the rainy season that decomposition processes are most significant with regard to the disappearance of organic material and the liberation or removal of nutrients from the litter layer.

In the dry season, following the initial leaching of soluble materials, both organic and inorganic[45], as well as the microorganism activity, there was very little macro-arthropod activity and root penetration. Decomposition was, therefore, carried out principally by the microorganisms and was slow.

In the wet season, besides initial leaching being much more intense, which we presume is also true of initial microorganism attack, there is the rapid and efficient action of the macro-arthropods, especially termites, removing a large part of the decomposing material. The volume of roots penetrating the material is also much greater. Both roots and macro-arthropods remove considerable quantities of nutrients from the litter but, on the other hand, they also deposit some minerals from the soil and plants, such as nitrogen, sulphur, zinc, and principally, iron and aluminum.

In conclusion, leaching appears to be the factor responsible for the loss of only some of the more soluble elements, such as potassium and boron, whereas macro-arthropods are responsible for the removal of the majority of the other mineral constituents from the leaves. Mineral cycles in terra-firme tropical forests are extremely complex and dependent to a high degree on biological activity for the decomposition of organic material and the liberation of the nutrients it contains.

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Primate communities in Amazonian forests: their habitats and food resources

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Introduction

Neotropical primates are forest dwellers and a large number of them occur in, or are restricted to the forests of the Amazon river basin and the Guianas (hereafter referred to as Amazonia). The most recent taxonomic revisions identify 43 primate species in this region (out of 65 for the whole neotropics), belonging to 14 of the 16 extant New World primate genera [51–53, 97]. These species are not uniformly distributed throughout Amazonia and most of them have restricted distributions, most frequently delimited by rivers, notably the Rio Solimões-Amazonas, Rio Negro, Rio Japurá-Caquetá, Rio Juruá, Rio Madeira and the Rio Tapajós[10, 51, 135]. Only three genera include sympatric congeneric species (*Saguinus, Cebus and Callicebus*), otherwise primate communities within Amazonia are composed of single representatives of each genus. The number of genera included in a community can be as many as 12, for example in the middle and upper Amazon Basin in northwest Brazil and Peru[96, 140] and according to known and supposed distributions, forests south of the Rio Solimões between the Rios Javarí and Juruá may include as many as 15 sympatric primate species. The study of the ecology and behavior of Amazonian primates has received little attention, although the situation has improved considerably since the early 1970s[106, 149]. With information from recent field studies and studies of the same or closely related species outside Amazonia, this review examines the ecological and behavioral differences between Amazonian primates in order to see how a community of 15 species, for example, share or divide up the food resources and habitats available in what is broadly termed the Amazonian tropical rainforest.

Habitats

Distribution maps of Amazonian primates give an erroneous impression of the homogeneity of the presence of a particular species within its range. There are a great vari-