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On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil

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Summary. The dynamics of the forest to the north of Manaus is tightly linked to that of the soil. The latosol that covers the plateau, which supports a dense forest, consists from top to bottom of: (a) a brown, clayey organic horizon (0.3 m), (b) a yellow horizon, very rich in clay but permeable (from 0.3 to 4 m), (c) a nodular horizon rich in Al and Fe oxides (from 4 to 9 m), and (d) a horizon which still preserves the sedimentary structures of the parent sandstone, where quartz is intensely dissolved and kaolinite crystallizes in pores. In perfectly flat areas, the clay of the organic horizon is destroyed by acidocomplexolysis, and the dissolved Al is transported vertically by the drainage water. A part of this Al is used to make the gibbsite nodules of horizon (c), and the rest is used to make kaolinite in horizon (d). Because aluminum is thus conserved within any vertical prism, the rate of destruction of horizon (a) is equivalent to the rate of advance of the kaolinization zone into the sediment: the latosol is said to be in equilibrium, the surface remains perfectly flat as it slowly sinks, the quantity of kaolinite increases with time, and the silica released by quartz dissolution in the whole profile is exported by drainage water to the water table. In contrast, near drainage axes, however small initially, the drainage becomes inclined toward the axis. Part of the Al released by acidocomplexolysis of horizon (a) is now exported to rivers, and Al is no longer conserved within any given prism. The rate of advance of the kaolinization zone (d) into the sediment now becomes less than the rate of destruction of horizon (a) and the surface sinks faster than that of the surrounding plateau. After this differential 'podzolization' has gone on long enough, it creates a network of 'geochemical valleys' characterized by convex slopes and bounded by sandy soils (campinas). The vegetation becomes sparser and sparser. At the end, only some bushes and lichens survive on the white sand.

Key words. Rain forest; sediment; latosol; podzol; geochemical land morphogenesis; dynamic equilibrium and disequilibrium; aluminium; silica.

The region to the north of the Amazon, between the rivers Rio Negro and Trombetas (fig. 1) is covered by a dense, humid, evergreen rain forest that has developed on yellow, clayey latosols.

The soils cover plateaux of the tertiary continental 'Barreiras' sediments. These plateaux are more or less strongly dissected by the hydrographic system (Planalto dissecado, Rio Trombetas, Rio Negro)[6]. The experimental station for forestry of the Instituto Nacional de Pesquisas da Amazônia, where this study was carried out, is about 60 km north of Manaus (see fig. 1) and is representative of the region.

These soils have as parental material the products of the weathering of the sediments (Barreiras formations), which involves intense dissolution of quartz, concentration of aluminum hydroxide, and crystallization of kaolinite in dissolution voids[9]. It turns out that these sediments, and even more their alteration products, are very poor in nutrients (phosphorus, calcium, potassium). The development of a dense forest on soils chemically so poor poses a problem which has attracted the attention of investigators[22].

At certain points along the edges of valleys variations exist in the density of forest cover[11,13]. These variations are slight near the heads of first-order valleys, and they become progressively greater down the valleys, as the hydrographic system becomes more branched. Ultimately one reaches open areas, called 'campinas', which contain quasi sterile spots of shrubs and lichens. Between the dense forest and these campinas there is a gradual transition ('campinarana') which is under study[11].

Concerning the pedologic cover, it has been established that the open areas or campinas are on white sands, which are sometimes several meters thick. Klinge[14] showed that these were podzols A2 horizons and that these soils have gradational contact with the flanking latosols developed on the tertiary sediments carrying rain forest. The transition is marked by 'leached' soils that Klinge[14] calls 'sandy bleached brown loam' and 'eluviated brown loam'.

When dealing with the origin of these soils, Klinge[14] showed also that the white sands of the podzols can, in some cases, develop at the expense of the eluviated brown loam. This led him to think that the parent material of the eluviated brown loam and therefore of certain podzols is a fluvial sediment deposited at the edges of the valleys, which is sandier and more recent than the Barreiras sediments.

Recently Lucas et al.[17] have studied this transition taking account of all the variations, vertical and lateral, of the pedologic cover, from the latosol of the plateaux along the valley heads to the podzols located at the edges of first order valleys. Their study shows that the whole constitutes a 'transformation system'[5] in which the latosol is progressively replaced by podzols.

This transformist interpretation has made us pay attention to two sets of observations and measurements carried out by several authors. The first studies refer to the role of man's impact on the differentiation of these soils and their vegetation. In the transition zone the eluviated brown loam (which usually has a sandy-clayey, brown-black surficial horizon, named 'terras pretas') supports a rather depressed forest vegetation (campinarana). This zone often contains denuded spots (campinas abertas) whose soils have widespread ceramic shards[19,25]. The evidence from pottery shards and radiocarbon dating of charcoal deposited in these soils demonstrate that the campinas were occupied and cleared by indians of the Guarita subculture around 800 A.D.[19]. The reforestation after indian clearing is extremely slow because of limiting

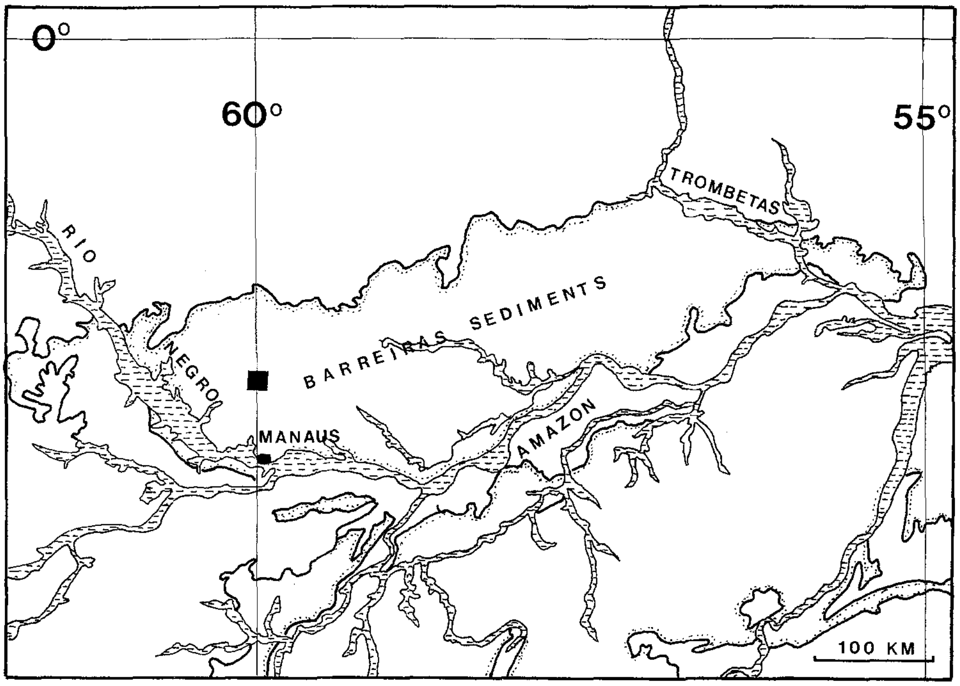

Figure 1. Locality map and studied area (■)[9]. (Fig. used with permission)

factors, such as nutrient deficiency and water conditions[19]. This means that man interfered in the past at places where conditions were favorable to him (less dense vegetation, which made clearing easier; organic and sandy soils, easier to work), but where there was already a natural disequilibrium that later held back the reconstitution of the forest. (The structural reconstitution of the forest requires, after even temporary farming, thirty or so years on the plateau latosols, though the full reconstitution of the variety of the flora may require much longer)[11].

Other studies deal with the relation between the evolution of the soil mantle and the composition of the waters of the stream that drain it. River water coming from podzols (campinas) is always brownish 'black water' ('coca-cola river')[16], whereas the waters coming from basins dominated by plateau latosols are clear[15,23]. The hydrochemical analyses[24] show that the black waters, colored by humic matter, have an extremely low inorganic ion content, whereas their concentrations of silica and aluminum are about 2.7 ppm and 300 ppb respectively. The clear waters contain a little more silica (4.5 ppm) but practically no aluminum (zero to traces). A quick evaluation taking account of the water balance[21] shows that for 1 km of drainage basin, about 2 or 3 tons of silica per year (for the black and clear water respectively) and 0.2 tons of aluminum per year (only for the black waters that come from the podzol cover) are exported.

Litology, climate, topography

The Barreiras group consists of cross-bedded arenites with intercaled argilites. The arenites are white to purplish red. The main constituents are quartz and kaolinite. Some beds have up to 5% feldspar and muscovite[6].

The climate is tropically hot. The average rainfall for nearby stations is about 2400 mm. Estimates of potential evapotranspiration are about 1500 mm/y[29]. The amount that feeds water table and rivers is thus of the order of 900 mm/y.

The block diagram of figure 2, obtained by photo-interpretation, shows that between the plateaux (P) and the valley bottoms (V) there are often intermediate surfaces (IS), which are slightly inclined toward the axis of the valley and which end in a short, steep slope. The more important and the more branched is the adjacent valley, the better developed, longer and lower at its downstream end are these intermediate surfaces.

The topographic cross sections accompanying the block diagram show the evolution of the slopes from upstream to downstream:

- The shorter section A is at the head of the valley; the convex slope is continuous with the plateau, and its lower end is about 25 m lower than the plateau.
- Section B, about 500 m from A, already begins to show an incipient intermediate surface (Is1), but one which is still continuous (that is, one whose slope changes monotonically);
- Section C, located between two secondary streams, is more than one kilometer long; its intermediate surface, slightly inclined, is here distinctly separated from the plateau by a saddle (a second intermediate surface, IS2, starts to develop up the slope from the saddle);
- Section D, significantly longer (1.5 km), shows a clearly individualized intermediate surface whose lower part has sagged. The flat valley reaches a depth of as much as 50 m below the plateau (in this valley, water discharge takes place mainly underground).

The sagging displayed by the best developed intermediate surfaces (section C and D) in their lower part precisely

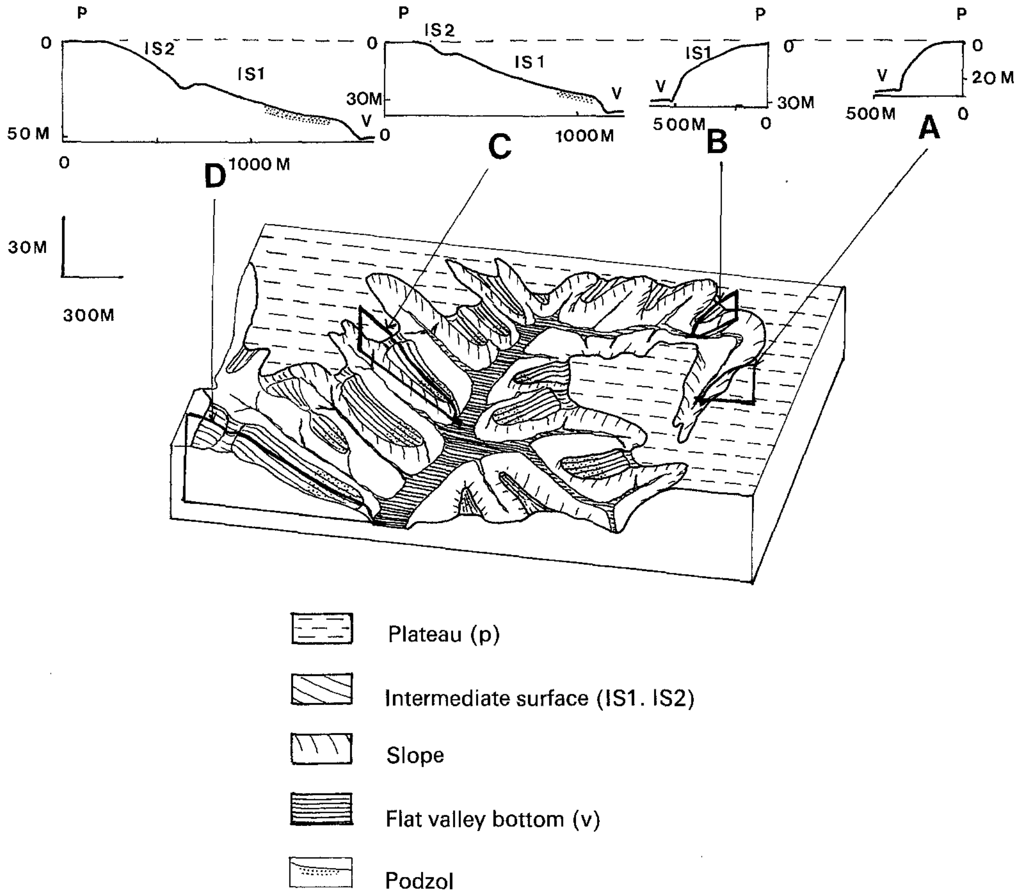

Figure 2. Block diagram showing the zone where podzol have developed[9]. (Fig. used with permission)

corresponds to the zone where podzols (shown by dotted lines on fig. 2) have developed.

The soils

The yellow clayey latosols of the plateaux are the 'latossolos amarelos, alicos, textura argilosa' of the Brazilian classification[7,8,20]. They correspond to the 'sols ferrallitiques fortement désaturés en B' of the French classification[2] and to the 'aplic acrorthox' of the Soil Taxonomy[10]. Under a thin (2–3 cm) bed of dead leaves, these soils have a brown organic horizon (A), about 30 cm thick, which grades downward into weakly structured, plastic horizons which are first brown-yellow and then yellow. The soil is clayey from the surface (with 65–75% of clay in the first 30 cm) and very clayey below down to 2–4 m of depth (with 80–90% clay); pH values measured in water are 4 to 4.5 down to 30 cm of depth and go up to more than 5 in the lower part of the profile. The sum of exchangeable bases (Ca^{++}, Mg^{++}, K^{+}, Na^{+}) is very low, about 1–2 meq/100 g in the A horizon and about 0.2 meq/100 g at depth. Exchangeable aluminum (Al^{+++}) is relatively high in the A horizon (2–4 meq/100 g) and goes down to 0.1–1.5 meq/100 g below. Available phosphorus is only appreciable in the A horizon (2–5 ppm, according to Olsen's method, 1954).

On the intermediate surfaces the whole spectrum can be observed from the yellow clayey latosols, through the 'eluviated soils', to the white sandy podzols[14]. The eluviated soils are the 'podzolicos vermelho-amarelo latossolicos' of the Brazilian classification[7]. They correspond to the 'epiaquic paleudults' of the Soil Taxonomy[10]. Under a bed of dead leaves of 2–3 cm, the A1 horizon (down to 18 cm) is brown gray black to dark brown. This grades downward into an A3 horizon, 30 cm thick, with organic brown spots, followed by a light brown B1 horizon 20 cm thick, a reddish yellow B2 horizon 1.6 m thick, and a pink B3 horizon with ferruginous reddish spots. The soil is clayey sandy (30% clay) in the A1 horizon, definitely clayey (with 45% clay) in the B2 horizon, and clayey sandy below a depth of 2.2 m. pHs measured in the water differ from those in the latosol in passing through a minimum (4.3) in the B1 horizon. The sum of exchangeable bases (Ca^{++}, Mg^{++}, K^{+}, Na^{+}) is very low (about 0.3 meq/100 g in the A1 and A3 horizons and 0.2 meq/100 g below). Concentrations of Al^{+++} are of the order of 1 meq/100 g in the A1, A3 and B1 horizons, and between 0.4 and 0.3 meg/100 g below. Available phosphorus is present only in the A1 horizon (2–5 ppm).

The podzol corresponds to the 'podzol alico' of the Brazilian classification[7] and the 'Arenic tropaquod' of the Soil Taxonomy[10]. The bed of dead leaves starting to decompose can reach 5–10 cm at the foot of the trees or be locally absent. The A1 horizon is black to dark gray and has variable thickness (0–30 cm) from place to place. The white to gray A2 horizon can be up to several meters thick; its boundary with the underlying dark brown spodic horizon (Bh Fe horizon) is sharp and irregular. The soil is on the whole sandy, the amount of clay being less than 5% in the Bh Fe horizon. The pHs measured in the water are less than 4 in the A1 and B2h horizons and between 4 and 5 in the rest of the profile. The sum of exchangeable bases (Ca^{++}, Mg^{++}, K^+, Na^+) is only appreciable in the horizon A1 (0.2–2 meq/100 g). Exchangeable aluminum (Al^{++}) is abundant in the A1 and B2h (Fe) horizons (3–8 meq/100 g). Available phosphorus is also concentrated in the same organic horizons A1 and Bh (4–10 ppm).

These data make it clear that considerable differentiation has taken place, both vertically (in the transformation of the sediment into a mantle of argillaceous latosol) and laterally (in the passage of this argillaceous latosol to the sandy podzols of the intermediate surfaces). These variations correspond to sequences which we now examine.

The vertical sequence from the sedimentary rock to the clayey latosol

This sequence has been studied at the center of small plateaux on cuts 15–18 m deep near the road 'Manaus-Boa Vista' (BR 174). These profiles consist, from base to top, of 3 main layers: (1) below 9 m, the parent sediment and the early stage of transformation; (2) a ferruginous and aluminous nodular layer about 5 m thick; (3) the clayey yellow latosol.

The parent sediment (Barreiras group) mainly consists of heteromatrical quartz grains associated with opaque grains of magnetite and a few zircon grains. These skeletal grains are irregularly scattered among a kaolinite plasma (about 30% kaolinite).

One can observe that the sediment has undergone mineral and structural transformations:

– Weak plasma ferruginization: the iron oxi-hydroxides are redistributed around skeleton grains and voids;

– Quartz dissolution; it becomes noticeable with the formation of peripheral voids between quartz and ferruginous plasma;

– Kaolinite neoformation: macroscopically the kaolinite neoformation is revealed by the occurrence of horizontally oriented white lenses of varied dimensions (millimetrical to metrical). Such white lenses are almost quartz-less and consist of kaolinite. Under the microscope, one observes the distribution of this kaolinite in booklets, which may reach 500 μm in the maximum dimension. This indicates automorphic growth of kaolinite. Moreover such kaolinite can penetrate the corrosion vugs, affecting the quartz grains. This demonstrates the neoformation of kaolinite as being simultaneous or posterior to the beginning of the quartz dissolution.

Thus, progressive and continuous transformations of the sediment appear and develop upwards in the profile. Such transformations result in a redistribution of iron oxides, a decrease of quartz content and an increase of kaolinite by neoformation (up to 60% of kaolinite). The quartz grains are increasingly replaced and engulfed by kaolinite plasma toward the top.

The nodular horizon, from a depth of 9 m to a depth of 4 m, is characterized by the formation and progressive evolution of several phases:

– Some of these phases become more and more indurated from bottom to top in the form of nodules of between 1 and 5 cm in diameter. These phases include (1) purplish red, iron-bearing nodules which are formed by ferric reprecipitation around voids while quartz grains dissolve, and (2) aluminum-rich nodules cemented by gibbsite and almost devoid of quartz (the crystallization of gibbsite in voids left by dissolution of quartz indicates supply of aluminum).

– Another dominant phase occurs which is loose and pinkish beige, consists of very fine kaolinite, ferric hydrates, and quartz, appears as branched tubes and becomes more developed from bottom to top until it occupies three fourths of the volume. At the top of the nodular level it passes into a yellow argillaceous micro-aggregated material.

A study of the order of differentiation of the various phases (nodular and loose) is in progress. The overall result is an increase in the amount of very fine kaolinite (80%).

The latosol, from a depth of 4 m to the surface, has been described above. Essentially argillaceous, it contains > 80% kaolinite, 2% ferric hydrates, 5–8% of gibbsite and a little quartz (10%) and zircon. Between a depth of 30 cm and the surface, in the A horizon, quartz increases (20%) and gibbsite tends to disappear.

The study of this vertical sequence reveals an ordered succession of structural and mineralogical transformations whose interpretation is discussed in the last section of this article.

The lateral sequence, from the clayey latosol to the podzol

The pedological approach used for this study is based on a detailed structural analysis of the soil mantle of an entire slope (intermediate surface). However, the toposequence studies are only two-dimensional analyses of the soil mantle and prove insufficient for explaining and illustrating the real, three-dimensional organization of the soil mantle. To approach this three dimensional structure it seems necessary to take into account all the vertical and lateral variations detectable in a set of four sections oriented along the line of highest slope (sections A, B, C, D, in fig. 2), following the method presented by Boulet et al.[4]. In this way it has been possible to arrange the different units studied in a genetic sequence, schematized in a few stages. This genetic sequence has been described by Lucas et al.[17].

Section C (figs 2 and 3) presents a well-developed intermediate surface, separated from the plateau by a saddle. Going from the latosol down towards the valley, one can observe an ordered variation of pedologic properties that can be summarized as follows: 1) gradual decrease of clay content at the base and top of the profile, as shown by the 'iso-clay' contours of figure 3 B; only the central horizon has 80% clay; 2) occurrence and then absence of ferric nodules at depth; 3) darkening of the humus-rich horizon at the surface, and occurrence of a break in the vertical distribution of organic matter; 4) superficial accumulation of organic matter not tied to mineral matter (called 'mor'; 5) differentiation of a sandy surficial horizon; 6) occurrence, at a small depth, of a dark brown horizon (Bh) where humic matter carried in solution from the

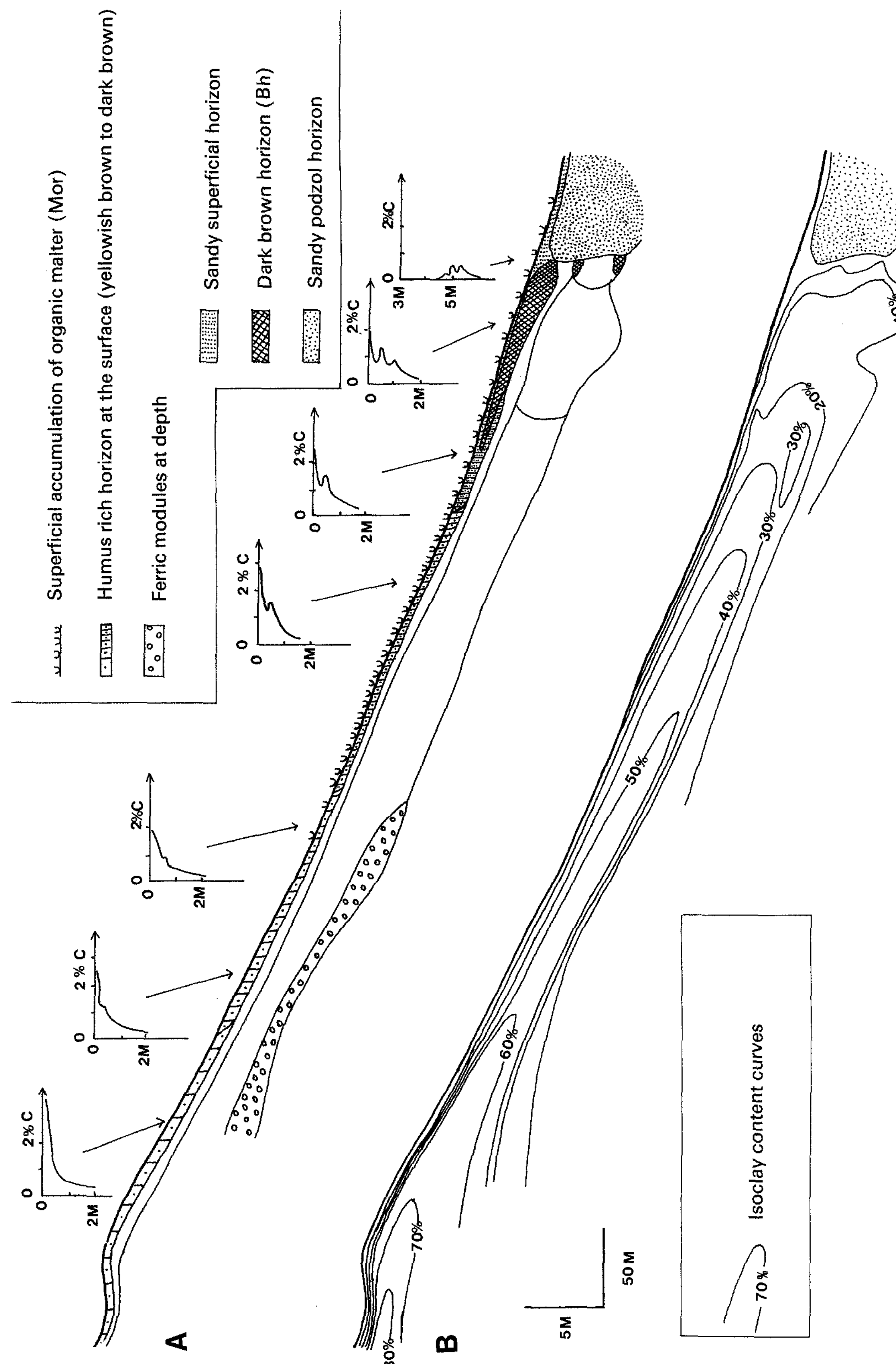

Figure 3. Soil mantle organization (*A*), vertical distribution of carbon, and isoclay-content curves (*B*)[9]. (Fig. used with permission)

surface has precipitated; 7) rapid decrease of clay content and lightening of the color; 8) superposition of several horizons of accumulation of humic matter (Bh); 9) bleaching and transition ot the sandy podzol as the brown horizon of humic accumulation (Bh) deepens.

The iso-clay-content curves (fig. 3 B) show that the decrease in clay takes place in both the upper and lower parts of the profile; this causes the volume with the same clay content to be tongue-shaped. There is no correlative clay enrichment in the intermediate horizons, which indeed become gradually poorer down the slope.

On the detailed section of figure 4 showing the passage to the white sandy podzol, one can see a yellow-red, sandy-clayey horizon (1) which is the last stage of this gradual decrease in clay content. This horizon ends laterally in tongues lined by chemical accumulations of organic matter (Bh), and locally of iron (B Fe), black to ocher brown (2). The horizon of white sand (3) is wedged under the yellow red horizon, and is underlain by another discontinuous horizon of organic accumulation (4) which is itself underlain by a white clayey-sandy material without visible porosity (5). A seasonal perched water (6) table forms during the rainy period in the white sands, above the white clayey-sandy material without visible porosity. There is a close relationship between the textural and organic differentiation of the profiles. In the clayey latosols up slope the vertical variations in clay content and organic matter are always gradual. Down slope considerable textural gradients and organic accumulation (Bh) appear and develop at varying depths. The works of Turenne[28] in Guyana and of Volkoff et al.[30] in the region of Manaus show that to this differentiation of the profiles corresponds a change of 'organic molecule structure' in relation to pedoclimate variations. The stable products having a high molecular weight (30,000), become dominant in the clayey, well-drained latosols up slope. As temporary and localized hydromorphic conditions develop down valleys, the organic substances quickly resolve into different more soluble components of a lower molecular weight (3000). The organic components of a low molecular weight could be responsible for the acidocomplexolysis of clays[18] (or cheluviation) [27] and for the formation of the Bh horizons.

Section B (fig. 2) shows an intermediate surface which is shorter than section C's and which is continuous with the plateau. The variations observed in that surface B[17] are only those present in the higher part of section C. A comparison among the four sections (A, B, C, D) shows that, as the intermediate surfaces become more developed, the genetic sequence become more complete in the direction of the podzol.

In fact, on section C and especially on section D, one can see that a second intermediate surface (IS2) starts to develop up slope from the original one (IS1), and also at the expense of the plateau.

Discussion and conclusions

The study of the vertical sequence from the sedimentary rock to the clayey latosol of the plateau has revealed an ordered succession of structural and mineralogical transformations which lead to the formation of a pedologic mantle several meters thick, essentially made up of kaolinite and a little gibbsite. It is only in the upper 30 cm of these soils that quartz becomes relatively significant by accumulation, whereas kalonite and gibbsite decrease slightly.

An experiment was carried out by Cerri and Chauvel at the CENA USP (Centro de Energia Nuclear na Agricultura, University of Saõ Paulo) laboratory to provide a better understanding of the causes of this impoverishment in clay. Distilled water was made to percolate through several soil samples (sieved but not dried) taken from the different horizons of the soil. Chemical analyses of the aqueous solutions issuing from the soil samples indicate: 1) a significant export of aluminum (7–30 ppm) only from the horizons in the uppermost 30 cm of the profile; 2) an export of silica (of 1–5 ppm) from all the horizons. These results allow one to suppose that the production of light organic compounds in the acid (pH) 4–4.5) surface horizons (where most biological activity is concentrated) is intense enough to drive the acidocomplexolysis (or chelation) of part of the kaolinite and gibbsite, with the water carrying away in solution the silica and aluminum released. The extraction of silica from other horizons would result only from quartz dissolution. The drainage of these soils being vertical, these solutions go through deeper horizons where the pH > 5. The aluminum then forms gibbsite in the nodular horizon, between the depths of 4 and 9 m, further down in the upper part of the parent sediment, the remaining aluminum contributes to the crystallization of kaolinite by reacting with silica released in situ by quartz dissolution.

The silica left over is exported in solution to the water table and the rivers. This explains why the export of elements from the system by rivers of clear water (which comes from latosols), calculated using Sioli data[23,24], amounts to 2–3 tons of silica/km^2, but only to traces of aluminum.

In sum, there takes place a slow and progressive destruction of the pedologic mantle near the surface, as well as a deepening of this mantle at the expense of the parent sediment. The rate of destruction of the soil being less than or equal to the rate of deepening, the pedologic mantle is in equilibrium in the sense of Boulet[3]. Nutrients are retained and accumulate in the top horizon and are

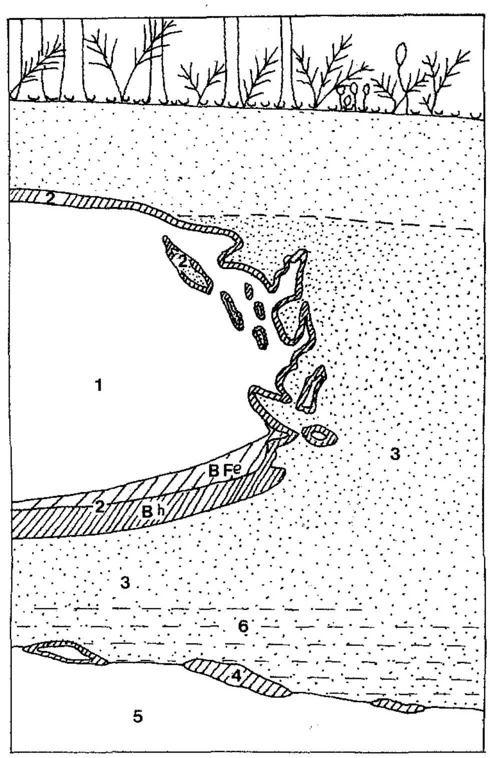

Figure 4. Detailed section showing the passage to the white sandy podzol[9]. (Fig. used with permission)

recycled once and again by plant and fauna activity. This explains the existence of a dense forest on soils formed from a nutrient-poor parent rock.

The study of the lateral sequence from the plateau latosols to the podzols reveals an ordered succession of pedologic organizations. Furthermore the comparative study of sections A, B, C and D shows that this sequence is all the more complete, the more branched and important the drainage axes become. These observations probably imply that an integrated hydrodynamic process causes the differentiations observed.

Going from the plateau towards the drainage axes one sees on the intermediate surface a set of transformations which affect both the inorganic constituents (gradual decrease in clay content at the top and the base of the profile, formation and destruction of ferric nodules, vertical changes in porosity, etc.) and the organic constituents (passage of an organic matter intimately mixed with clay or 'mull' to an accumulation of incompletely decomposed plant debris or 'mor', increasing migration of humic acids carried in solution and precipitated at various depths in dark brown or black Bh horizons, etc.). Further downhill the B 2 horizon becomes surrounded on all sides by accumulations of organic matter (Bh) and locally of iron (B Fe). The B 2 horizon ends sharply and gives way to white sand podzol, which is subjected to the action of a temporary and fluctuating water table.

This transformation of the organic matter could result from a lateral variation of the pedoclimate linked with lateral water percolation in the slope, and/or from changes in the physico-chemical conditions in the intermediate surface. Regardless of the exact cause of this transformation, it is clear that the increased migration of free humic acids is accompanied by a decrease in the clay content and by a redistribution of iron oxides. It is therefore very likely that the humic acids cause the destruction of clay by acidocomplexolysis[18].

Thus the pedologic cover is progressively destroyed from the head of the intermediate surface. This destruction is at first weak, and is localized in the top and the base of the latosol, and then progressively downhill, as it is caused by the lateral water flow in the direction of the drainage axes. Part of the dissolved aluminum and silica probably feed the growth of neoformed kaolinite. The remainder is carried away to the water of the black rivers, as shown by the evaluation made above, based on Sioli's data[23]; about 2 tons of silica and 0.2 tons of aluminum are exported per square kilometer per year.

The rate of destruction of the soil mantle (at its top and at its base) progressively becomes greater than its rate of deepening. This disequilibrates (in Boulet's sense)[3] the latosol, which wedges out. The sandy podzol then develops directly on the alteration products of the underlying sediments. The mobilization of organic constituents and the acidocomplexolysis of clays release nutrients, which are initially held by the clayey, humus rich horizons. The vegetation becomes sparser and sparser, and passes from dense forest to campinarana to campina aberta. At the end only some bushes and lichens survive on the white sand.

In spite of the fact that the natural rate of evolution of these systems is slow in human terms, it appears[5] that these pedologic mantles out of equilibrium are fragile and can become very rapidly degraded where man takes no account of their specific dynamics.

This is a progress report on the dynamics of Central Amazonian soils and forest. Laboratory and field work is under way to better characterize the morphological, chemical and mineralogical aspects of this dynamics.

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Some structural and floristic aspects of the forest

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Key words. Vegetation type; forest structure; floristic composition; swamp forest; campina; campinarana.

1. Introduction

In flying over the Central Amazonian forest, one would certainly be tempted to describe the landscape as homogeneous if not monotonous. Apart from the water surfaces of the large rivers, it is a uniform, dark green carpet, rippled by innumerable smaller rivers and streams.

However, in penetrating this forest along streams and trails, one observes that, in fact, it represents a mosaic of distinct structural entities. To begin with, there are three main categories of forest: first, forest which is periodically inundated by white water (carrying sediments) of the Amazon River (known as 'várzea'); the second type is forest inundated by the blackwater rivers ('igapó') containing dissolved humic acids as in for example the Rio Negro; the third type of forest is that of the so-called 'terra-firme', i.e. upland, which is not subject to periodic inundations by the big river systems.

To prevent misunderstanding, it must be stressed that this study concerns only the last category of forests. We use specifically the term forest on terra-firme as defined by Prance[22] for the forest of a well-drained plateau and of slopes descending towards stream beds ('baixios').

Following the few studies already made on the natural vegetation of the terra-firme, as opposed to igapó and várzea, and according to several years of our own observations, four major forest types may be distinguished: terra-firme forest in the restricted sense; 'campina'; 'campinarana'; and swamp forest. Although these four forest types are functionally related, each exhibits its own structural and functional characteristics, which, for purely methodological reasons, will be presented separately. (The term 'structure' has been used in different ways[29]. Here it refers to the spatial organization, the second characteristic of an ecosystem is its functioning, that is, its organization in time[32].) Only structural characteristics, including floristic data, are presented here, and some aspects of interrelations will be considered at the end. Up to the present, human activity has had little impact; the forest landscape is essentially intact with the exception of small strips along the few roads and larger rivers with their secondary forests, and more or less cultivated areas in the immediate proximity of recent settlements. Secondary forests, the so-called 'capoeira', are excluded from this study.

2. Vegetation types

2.1. The forest on terra-firme

2.1.1. General organization. For the intact terra-firme forests of hydrographic basins such as the area we have studied at Reserve – km 60, which includes plateaux and slopes, it is possible to distinguish four vertical layers: trees above 15 m in height; trees from 12–15 m; small trees and shrubs from 7–12 m; and lower shrubs and saplings from ground level to 7 m.

Considering similar topographic sites, the top layer is remarkably homogeneous in appearance and includes two superposed structural 'sets of trees of the present' (in other words, 'trees that lack any potential for further expansion'), and one 'set of trees of the future' (or, trees that 'still have a potential for future expansion'[20]). This 'set of the future' may be absent in certain areas.

The second layer is variable in structure yet represents always one 'set of the present' or a 'set of the future', the foliage of which constitutes a neat and important trophic unit. The third and fourth layers are essentially homogeneous in their spatial pattern, but show a tendency towards simplification on the slopes in that the third layer is markedly more complex on the plateau.

These four layers result from the spatial distribution of erect and rigid plants such as trees, shrubs, palms, saplings as well as the ground herbs, which constitute the 'synusiae' of the mechanically independent autotrophs (a synusia being a group of plants 'of similar life-form, filling the same niche and playing a similar role, in the community of which it forms a part'[27]), and which present the skeleton for the synusiae of the mechanically dependent plants such as lianas, stranglers, epiphytes and heterotrophs, which distribute themselves according to their ecological needs and to the habitats available. We consider here only vascular plants. Little research has been done on non-vascular plants, bryophytes, lichens, algae and fungi, even though they are very common. Apart