



Soils and Soil Process Research

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Soils, together with correlative factors such as climate and topographic position, strongly influence plant growth, survival, and reproductive success. These processes determine, in turn, the composition and productivity of rain forest communities (e.g., Ashton 1964, 1976b; Webb 1969; Austin et al. 1972; Baillie et al. 1987) as well as the opportunities and constraints for agriculture and forestry (e.g., Sánchez 1976; Uehara and Gillman 1981). Thus, an adequate understanding of soil processes and properties is a prerequisite to any study of natural or managed terrestrial ecosystems.

Tropical soils are often lumped into a single category: red, infertile, and hardening irreversibly upon clearing. Nothing could be farther from the truth. The soils of the lowland humid tropics are as diverse as those of any other region. Some are, indeed, red and infertile. Some do harden irreversibly upon drying although these account for only about 7% of the tropical landmass (Sánchez 1976). But significant areas are occupied by young alluvial soils that are among the most fertile in the world. And young fertile soils are the rule throughout the volcanically active parts of the tropics where fresh, rapidly weathering mineral material is added constantly to the land surface. La Selva is, in certain regards, a microcosm of humid tropical soils. Although unusual in their physical properties, La Selva's soils span a large portion of the range in soil chemical properties found anywhere in the humid tropics.

Much information about the soils of the humid tropics has accumulated over the past few decades. To organize and use this information efficiently requires a soil classification system. Several are in use today in the tropics. Soil scientists in France, Brazil, and Australia have developed systems to use locally. A system developed by the Food and Agriculture Organization (FAO) has gained some international acceptance but provides only two hierarchical levels; thus, degrees of similarity among soils are difficult to judge. The only fully hierarchical classification system used widely is Soil Taxonomy (USDA Soil Survey Staff 1975, 1987, 1990). This system is used extensively within Costa Rica and elsewhere in Latin America and is used here.

Soil Taxonomy classifies soil mainly on the basis of diagnostic horizons (distinctive layers in the soil) and climate. Other criteria are used but vary widely with soil type and are too complex to describe here. In all, three soil orders are represented at La Selva: Entisols (young mineral soils lacking a B horizon), Inceptisols (relatively youthful soils with undistinguished B horizons), and Ultisols (well-weathered soils

with an accumulation of clay in the B horizon). For those interested in learning more about Soil Taxonomy, an excellent text is available (Buol et al. 1980) in addition to the primary descriptions (Soil Survey Staff 1975, 1987, 1990).

An important feature of Soil Taxonomy is that the names themselves convey important information about the properties of the soils and their positions within the taxonomic hierarchy. For example, one of La Selva's soils is classified as an Oxic Humitropept. The *ept* in this name indicates that the soil is in the order Inceptisol. The appearance of *trop* in the name tells one further that the soil occurs in the tropics. The *humi* indicates that it contains large amounts of organic matter and the *oxi* that it has weathered to the point where its capacity to retain cations is quite low. Other terms relevant to La Selva's soils include *fluv* (for fluvial), *aqu* and *aquic* (for wet), *lithic* (for stony or in contact with rock), *psamm* (for sandy), *eu* (meaning rich in base cations), *dys* (for poor in base cations), and *histic* (for an accumulation of mineral-free organic matter). The term *andic* (or *and*) comes from the Japanese word for black and refers to soils, generally of volcanic origin, with distinctive claylike minerals that give rise to unusual properties such as high organic-matter content and water-holding capacity. Lastly, the term *typic* means simply "typical." Sollins et al. (1988) discuss in more detail the ecological information that can be inferred from the names used in Soil Taxonomy.

Soil Taxonomy differs fundamentally from the Linnaean system of biological nomenclature and classification. Because of biological processes, organisms can be grouped into well-defined units, called species, with relatively few intergrades among them. Soils, however, grade continuously from one type to another. Because of this continuity, the borders between even the highest-level taxa (orders) must be drawn arbitrarily, which means that the correction of a small error in laboratory results or a slight change in sampling location on the landscape may shift a soil into a different order. Although sometimes disconcerting to biological taxonomists, who are accustomed to clearer distinctions, at least between higher taxa, the fact that soils span a continuum is an inevitable and challenging feature of soil classification.

Soil survey and classification organize information on the chemistry and physics of soils, which can then be used to predict nutrient availability and biological activity, especially as they change in response to weather and to land-use practices. In this chapter we first describe the current state of knowledge concerning soil survey and classification at La Selva. Next we

describe what is known of the chemical and physical properties of La Selva's soils. Last we place La Selva's soils in the context of tropical soils worldwide. Studies of soil biology and nutrient cycling and of the effects of soil processes on plant communities at La Selva are discussed elsewhere (chapter 5).

This chapter is intended to serve soil scientists and other researchers interested in working at La Selva and in comparing La Selva with other sites worldwide. It is impractical to try here to explain the basic concepts and terminology of an entire field of study (soil science plus large portions of geology and geomorphology). We have, however, attempted to define those terms that do not appear in standard dictionaries and whose meaning we feel is critical to an overall understanding of La Selva's soils and to write in a way that allows a reader to benefit from reading the chapter even if unfamiliar with the more technical terms. We would be most pleased if this chapter, coupled with a desire to research tropical terrestrial ecosystems, prompted some readers to dig deeper into the field. For those, we recommend general introductions to soils and nutrient cycling by Brady (1984) and Schlesinger (1991), more specialized texts and monographs by Sánchez (1976) and Uehara and Gillman (1981), and a particularly insightful essay on "Macrovariability of Soils of the Tropics" by Van Wambeke and Dudal (1978).

SOIL FORMATION AT LA SELVA

Soil scientists recognize five major factors of soil formation (Jenny 1941): climate, vegetation, topographic position, parent material, and soil age. La Selva spans only some 120 m of relief; consequently, climate is unlikely to have played a major role in creating soil variability at the site. Vegetation may have been an important influence, especially in the primary forest where canopy emergents persist for centuries and may create distinctive soil conditions under their canopies, but such effects have not yet been documented at La Selva. Topographic position is important locally at La Selva—distinctive soils have developed in poorly drained areas and along the small V-shaped streams—but, in general, parent material and soil age account for most of the differences between soil types at La Selva.

The nature of the parent material and soil age are determined by the nature and timing of the geomorphic processes that create the land surface. At La Selva, all parent materials resulted originally from volcanic activity. Ashfall, lahars (volcanic mud flows), and lava flows, three geomorphic processes unique to volcanic landscapes, have been important on the east slope of the Cordillera Central. At La Selva specifically, however, there is no evidence of ashfall. This lack is not surprising because the site lies well upwind of Costa Rica's volcanoes. (For example, as one moves westward from La Selva, the limit of subaerial ashfall is encountered about 2 km northeast of San Miguel toward La Virgen along the main highway from San José to Puerto Viejo [fig. 4.1].) Lahars, too, have played only a minor role in building La Selva's land surface. (Large areas of lahars are in evidence, however, east of the town of Río Frío toward Guápiles and to the north of the road between Chilamate and San Miguel [see fig. 4.1]) Lava flows, in contrast, have played a major role. Descending from the Cordille-

ran volcanos periodically during the last two million years, they have, at one time or another, covered almost the entire La Selva land surface. At the higher elevations, the flows have weathered slowly to form the so-called residual soils that we see now. At lower elevations, the lava flows were later covered over by alluvial and colluvial deposits.

Alluvial and colluvial processes operate in volcanic landscapes just as they do elsewhere. Lying atop the lava flows throughout the lower elevations at La Selva is alluvium deposited during overflow of the Río Sarapiquí and Río Puerto Viejo (fig. 4.1). These deposits can be presumed to span a fairly narrow range of mineralogy and chemical composition because all the material derives from flows and ejecta of the Cordilleran volcanoes and was well mixed during transport. Texture of the original deposits, however, appears to have varied considerably, depending on factors such as stream gradient and distance from the stream channel at the time of deposit. Because finer deposits weather faster than coarse ones, such textural differences have played a major role in determining the current state of the soils at La Selva.

Age is the other dominant factor determining soil properties at La Selva, especially for the alluvial soils. The alluvium was deposited as terraces, with the youngest occupying the lowest slope positions. The oldest terraces are widely regarded as Pleistocene in age, but dates are lacking. The lowest terraces flood periodically and contain an especially complex mosaic of soils because their properties are still so strongly affected by even small differences in age and original texture. The weathering sequence in this volcanic alluvium parallels in many ways those observed on lahars and volcanic ash deposits. Sancho and Mata (1987) referred to the terrace landscape as fluvio-volcanic to emphasize this point.

EARLY SOIL SURVEY AT LA SELVA

In the earliest reference to the soils of La Selva Petriceks (1956) divided Finca La Selva into red-brown lateritic soils occupying 85% of the area (613 ha), swamp soils (38 ha), and recent alluvial soils (35 ha).

In a second study researchers from the University of Washington distinguished three major landforms: two alluvial terraces (a lower and an upper) and an area of older soils toward the back of the property that they believed had formed in lava flows (Bourgeois et al. 1972). Modal profiles were described for nine soil series, all Entisols or Inceptisols, and samples were analyzed chemically.

In 1981 the Organization for Tropical Studies (OTS) began a conscious effort to stimulate ecosystems studies at La Selva. As part of these efforts, several investigators (G. Parker, M. Huston, P. Werner, P. Sollins, and P. Vitousek) carried out informal soil survey and classification in the areas where they worked. Such work set the stage for the first comprehensive survey of the soils of La Selva.

CURRENT SOIL SURVEY

In 1987 F. Sancho and R. Mata of the University of Costa Rica, under contract to R. Sanford and J. Denslow, surveyed the entire La Selva property. They described profiles by horizon based on standard soil survey methods (FAO 1968) at a

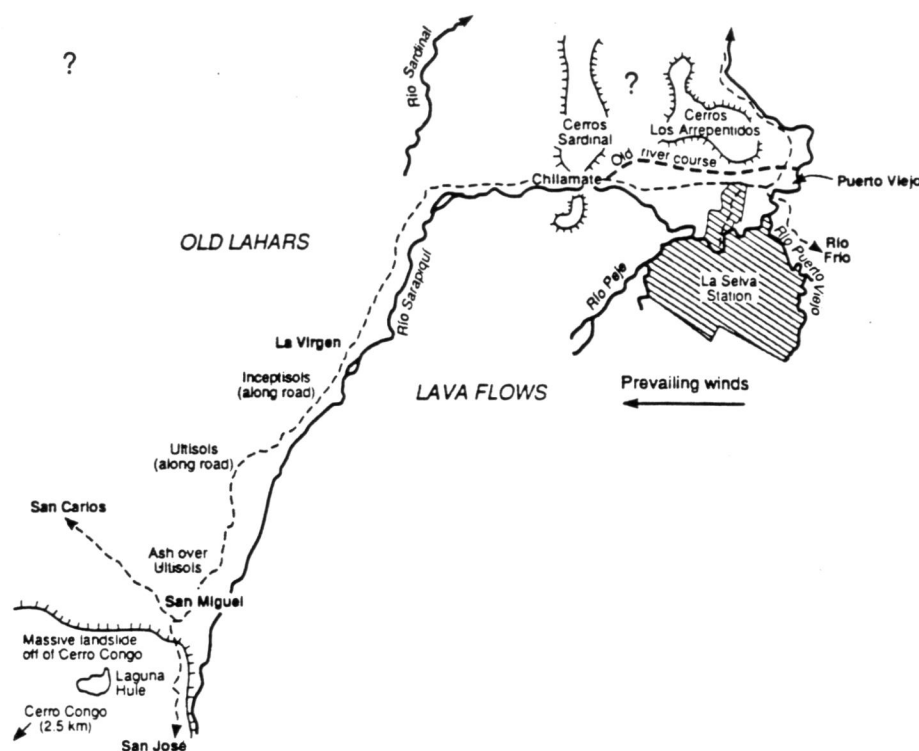


Fig. 4.1. The Sarapiquí region: major land-forms and soil types.

density of twenty-five observations per km^2 with a combination of pits (to 1.5 m depth) and auger holes (to 1.2 m depth). They then sampled the pits for subsequent chemical and physical analysis (table 4.1) and classified the soils according to the original version of Soil Taxonomy (USDA Soil Survey Staff 1975). Later, in 1989, two mapping units were resampled and reclassified according to the revised Soil Taxonomy (USDA Soil Survey Staff 1987, 1990).

Methods

Moisture content at -0.033 and -1.5 MPa was measured with a pressure plate on field moist, reconstructed cores and expressed on a unit dry-weight basis. Bulk density was measured with a coring device designed to minimize compaction. Parallel sampling of a subset of the pits with bulk density cans gave identical results. For all other analyses, soil was air dried and sieved (2 mm). Texture was analyzed by the Bouyoucos method after the soil had been treated with hydrogen peroxide to remove organic matter and dispersed by shaking for two hours with sodium hexametaphosphate. Designation of textural classes followed the rules of USDA Soil Survey Staff (1975). Soil pH was measured in water and potassium chloride (1 M) at a soil:solution ratio of 1:2.5. The pH in sodium fluoride was measured after two minutes. Organic matter (OM) content was measured by the Walkley-Black method. Oxalate-extractable aluminum and iron were determined by shaking 0.4 g of soil for four hours in the dark in 40 ml of extracting solution (mixture of ammonium oxalate and oxalic acid, 0.2 M with respect to oxalate, with proportions adjusted to give pH 3). Five drops of superfloc (0.4%) were added, the suspension was centrifuged (2,000 rpm, five minutes) and filtered (Whatman 42). The aluminum and iron concentrations in the supernatant were determined by atomic absorption spectrometry.

Cation exchange capacity (CEC) was measured with ammonium acetate (1 M) at pH 7 (USDA Soil Conservation Service 1972); the extract was analyzed for bases by atomic absorption spectrometry. For exchangeable acidity, samples were shaken for ten minutes in potassium chloride (1 M), filtered and titrated with sodium hydroxide (0.01 M). In the results shown in table 4.1, effective CEC (ECEC) was calculated as the sum of calcium, magnesium, potassium, and exchangeable acidity. Base saturation was then computed as the ratio of $\text{Ca} + \text{Mg} + \text{K}$ to ECEC.

Phosphorus data in table 4.1 refer to surface soil (0- to 15-cm depth) samples gathered by Sancho and Mata during their 1987 survey. Samples were collected from all pits and auger holes, extracted on-site with dilute acid ammonium fluoride, and analyzed for phosphorus colorimetrically (Vitousek and Denslow 1987). Not all extracts were analyzed.

On the basis of profile observations and soils analyses, Sancho and Mata (1987) mapped most of La Selva at a scale of 1:10,000. (The Peje Annex was surveyed but no map was prepared because no base map was available.) In their overall arrangement of soil types, they recognized the same basic landscape units identified by Bourgeois et al. (1972)—older soils developed from lava flows toward the back of the property, alluvial terraces along the major rivers (Sarapiquí, Puerto Viejo, and Peje), and depositional zones in low-lying areas along creeks. They identified a total of twenty-three consociations and one complex (fig. 4.2). (Consociations are mapping units in which a single soil type occupies at least 75% of the area; similar but different soil types comprise the remaining area. Soil complexes group two or more dissimilar soil types that occur together in regular and repeating patterns too intricate to warrant separation at the scale of the soil survey.)

In what follows, we discuss each consociation and the single complex, emphasizing how and why they differ. We

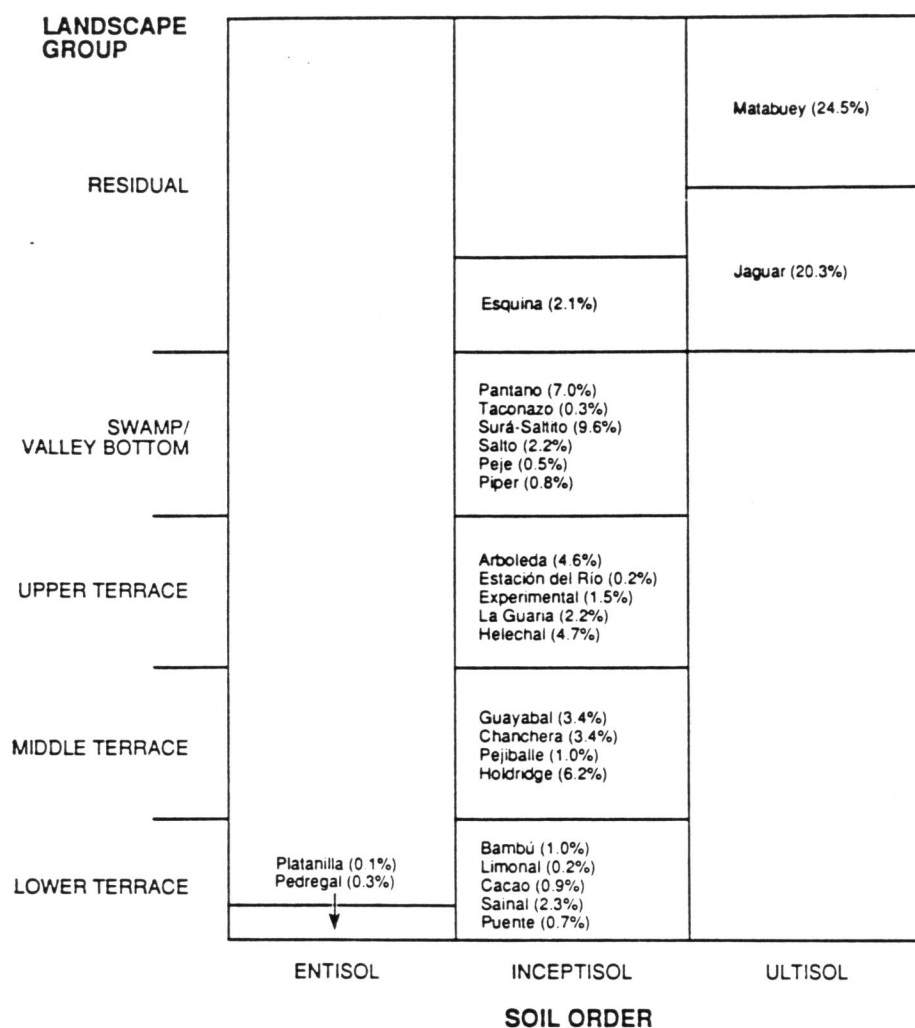


Fig. 4.2. Soil consociations and complexes at La Selva. Area of each block is proportional to logarithm of area occupied by the mapping unit. Values are for La Selva Biological Station only; many of these units occur also outside the station.

describe areal extent, parent material, landform, and topography as well as salient chemical and physical characteristics. Elevations, where known, come from a 1982 survey along major trail systems of La Selva (D. A. Clark pers. comm.) or from a 1984 survey of a portion of the La Guaria Annex. Sites of major research projects are located with respect to the mapping units on which they occur.

The boundaries, profile descriptions, and physical/chemical data presented here supersede those in the report by Sancho and Mata (1987). In the years since Sancho and Mata completed their survey, several boundaries and relationships between consociations have been better defined. Topographic information has been unearthed that was not available to Sancho and Mata at the time of their survey. The Helechal consociation, in particular, has been resampled and its boundaries redefined. Material in this chapter thus represents the state of knowledge as of summer 1991, but boundaries will continue to change and new mapping units may be defined as more researchers become familiar with the soils of La Selva. (In late 1992 a topographic survey was completed that will, no doubt, substantially alter mapping unit boundaries.)

The Residual Soils

Three lava flows—the Esquina (andesitic), Salto (andesitic/basaltic) and Taconazo (andesitic/basaltic) (Alvarado 1985)—

give rise to the major “residual” soil consociations of La Selva (here, “residual” means simply “derived from lava flows”). Sancho and Mata (1987) recognized one mapping unit (the Matabuey consociation) on Salto lava and three on Esquina lava: the Arboleda at the lowest elevations near the upper river terrace, the Esquina on a lightly scarped area in the extreme southern corner of La Selva, and the Jaguar on the remaining strongly undulating to lightly scarped terrain. The Arboleda soils are more likely very old alluvial soils. In addition, we now recognize that the Matabuey consociation, as presently defined, derives from both Salto and Taconazo lavas.

The Matabuey (bushmaster, the largest of La Selva’s poisonous snakes) consociation is the most widespread of La Selva’s soils (fig. 4.3). It occupies the hilly upland portions of La Selva except toward the center of Old La Selva, where it is replaced by the Jaguar unit. To the west it extends to (and presumably beyond) the Río Peje. Chemically, the Matabuey soils are strongly acid (see table 4.1), organic matter rich, and highly leached, with a low degree of base saturation (30%) and a fairly large amount of exchangeable acidity. The increase in measured clay content between A and B horizons meets the criterion for an argillic horizon; thus, the soils were classified as Ultisols rather than Inceptisols. None of La Selva’s Ultisols, however, show well-developed clay skins. Depth to C horizon varies. On steep slopes near the rivers, saprolite

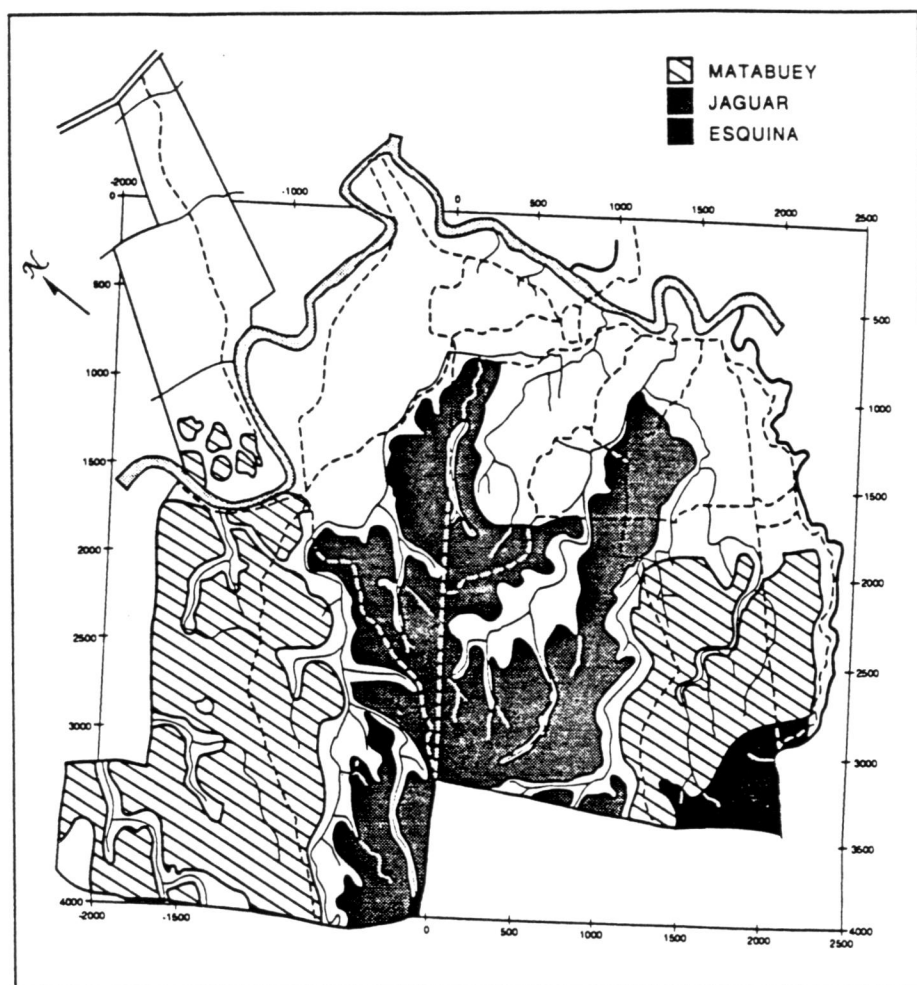


Fig. 4.3. Residual soils of La Selva: Matabuey, Jaguar, and Esquina consociations. Dashed lines on this and subsequent figures are major trails.

(highly weathered rock) outcrops at the surface. On ridgetops, however, B-horizon thickness can exceed 8.5 m (Parker 1985), an indication of the advanced stage of weathering of this soil. The majority of the unit was classified as a Typic Tropohumult because of its organic-matter content; inclusions are mainly Typic Dystropepts. Most of the TRIALS forestry plantations (see chapter 25) were established on hilly areas of Matabuey soils surrounded by younger soils derived from alluvial deposits. Studies by Luvall (1984) and Parker (1985) were conducted on Matabuey soils just outside the southern boundary of the Sarapiquí Annex.

The Matabuey unit, as described by Sancho and Mata (1987), occurs also near the Río Sarapiquí upstream from the ford and cable-car crossing, where it forms discontinuous cliffs along both sides of the river. It also occurs in hilly portions of the La Guaria Annex where the Taconazo lava flow was not (or is no longer) covered by upper-terrace deposits from which derive the soils of the Helechal consociation. Because the relationship between the Matabuey and Helechal units is complex, discussion is postponed to the end of this section after both units have been described.

The Jaguar consociation is the second most extensive unit at La Selva. Developed from the Esquina lava flow (andesitic), it occupies the central portion of the property between the Quebradas Salto and Surá see (fig. 4.3) and is bounded on

both sides by Arboleda consociation. Sancho and Mata (1987) found no chemical or physical differences between the Jaguar and Matabuey soils although they did note differences in color (see table 4.1). The two were separated mainly to maintain correspondence between lava flow and soil consociation.

Vitousek and Denslow (1987) compared P levels and plant growth on what they called "lava-flow-1" and "lava-flow-2" soils at La Selva. The "lava-flow-1" soil in their table 1 corresponds to the Jaguar consociation (plus Arboleda), their "lava-flow-2" soil to the Matabuey. For their plant bioassays (their table 2), lava-flow 1 corresponds again with Jaguar, but their lava-flow-2 soil came actually from a site within the Arboleda consociation. (Their old alluvial soil is in the Holdridge consociation.) All gaps used by Denslow et al. (1990) for outplanting experiments fell within the Jaguar consociation.

The Esquina (corner; name of creek) consociation is restricted to the extreme southeastern corner of La Selva (fig. 4.3) on the Esquina lava flow (andesitic). Except possibly for higher organic matter content, Sancho and Mata (1987) found no chemical differences between the Esquina unit and the Jaguar or Matabuey. Although the Esquina and Matabuey units derive from the same lava flow, the Esquina soils lack argillic horizons (for unknown reasons) and were, thus, classified by Sancho and Mata (1987) as Andic Humitropepts.

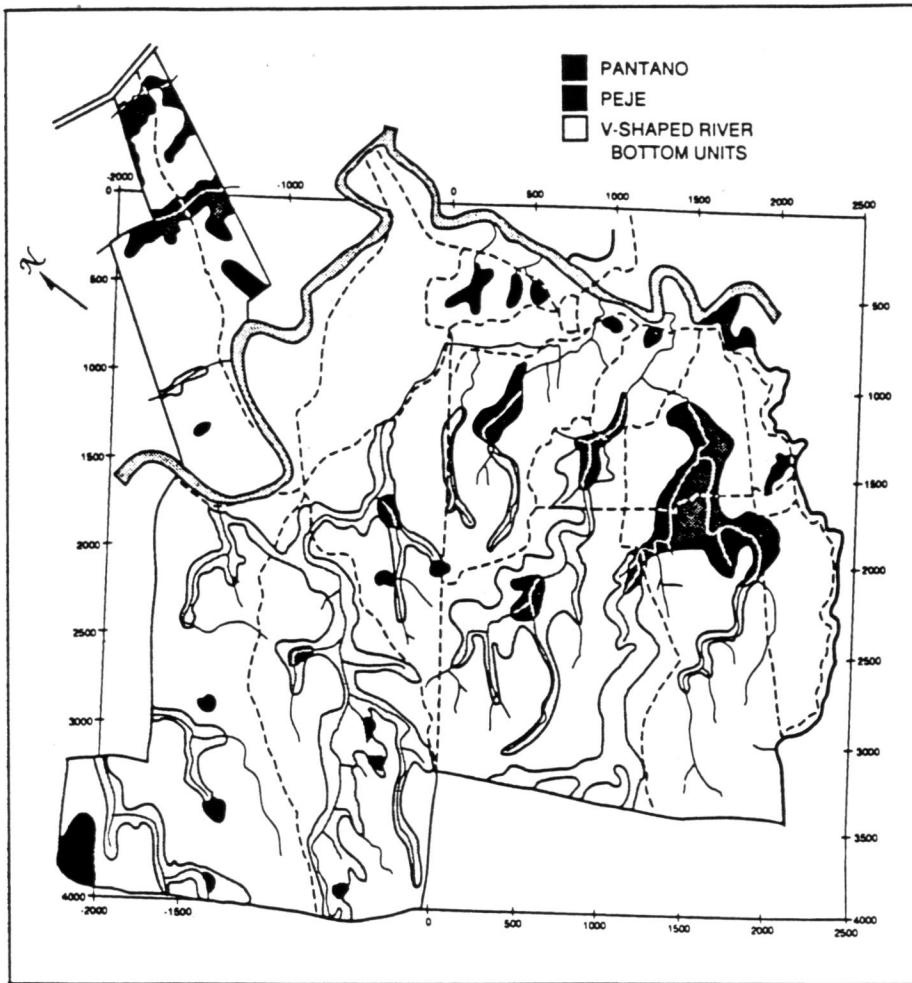


Fig. 4.4. Soils of the swamps and valley bottoms: Pantano complex, consociations of the V-shaped valley bottoms (Surá-Saltito, Salto, Piper, and Taconazo), and the Peje consociation (mainly off the map on the Peje Annex).

Soils of the Valley Bottoms and Swamps

Throughout the hilly to undulating landscape that has developed on the lava flows and upper terraces, streams have formed small V-shaped valleys with small depositional zones at the bottom of each. Soils along the Quebradas Salto, Taconazo, and Piper are distinctive; the rest are combined into a single consociation (Surá-Saltito) named for the two largest streams along which this unit occurs (fig. 4.4).

The Surá-Saltito consociation, which accounts for the majority of the valley bottom soils, is extremely acid (pH 4.0–4.2), OM-rich, and very base poor. The soils are clayey and of heavy texture, colors are brown to yellowish-brown, and drainage is moderate. Rocks outcrop on 5%–10% of the area mainly near the Quebrada Surá. Generally the B horizon extends below 1.2 m, but in places a C horizon was encountered at <1.2-m depth that consists of saprolite derived from weathered lava. The dominant soils of this unit are Typic Humitropepts; inclusions are mainly in Lithic and Aquic subgroups.

The Salto consociation is found only along the Quebrada El Salto, upstream of the area where the creek traverses soils of the Pantano complex (see below). Colors are dark brown to dark yellow brown, and drainage is poor to moderate. Surface soil is acid, very base poor, and rich in OM. The C horizon, consisting of rock and saprolite, is usually encountered at <50

cm depth, and rocks are abundant throughout the profile. The dominant soil is a Lithic Humitropept.

The Taconazo consociation is restricted to the margins of the Quebrada El Taconazo along the western border of the original La Selva property. The Taconazo unit along with portions of the Matabuey derive from Taconazo lava, the oldest of La Selva's parent materials (Alvarado 1985). Stones are abundant in the upper parts of the profile. Surface soil is strongly acid and base-poor. Gray colors below a 22-cm depth indicate poor drainage; in fact, the water table rises in places to within 50 cm of the soil surface. This soil yielded quite high levels of extractable phosphorus (table 4.1). The dominant soil is a Typic Tropaquept.

Soils of the Piper consociation are moderately well drained and stone free. The soils are notably low in clay, thus, very readily worked. The surface soil is much less acid (pH 5.2) than in the Surá/Saltito, Salto, or Taconazo units. Unlike the other valley-bottom soils, those of the Piper unit are rich in bases and organic matter and, thus, presumably quite fertile. The unit floods periodically. The dominant soil is a Fluventic Humitropept.

The Peje consociation occupies an aggrading, U-shaped flood plain along the Río Peje at the extreme western boundary of the Peje Annex. Unfortunately, no base map was available for the Peje Annex at the time of the soil survey, so the

Table 4.1 Chemical and physical properties of La Selva soils

Mapping unit	Profile No.	Classification	Horizon	Depth (cm)	Munsell Color	pH			Organic Matter (%)				KCl Acidity	Sum of Bases	CEC (NH ₄ OAc)	Base Saturation ^b (%)	P ^c (mg/kg)	Water Content		Bulk Density (Mg/m ³)	Clay (%)	
						H ₂ O	KCl	NaF		Ca	Mg	K						-3 MPa	-1.5 MPa			
						(cmol(+) /kg)																
Residual units																						
Matabuey ^a		Typic Tropohumult	A	0-18	7.5 YR 3/4	5.0	4.0	8.7	7.13	0.59	0.46	0.35	3.15	1.40	4.55	28.0	30.8	0.6	46.3	33.0	0.80	41
			Bt1	35-88	7.5 YR 4/4	4.8	4.2	9.7	2.70	0.53	0.21	0.19	1.85	0.93	2.78	20.1	33.4	—	38.1	31.2	0.84	62
Jaguar ^a		Typic Tropohumult	A	0-19	7.5 YR 3/4	4.5	4.2	8.6	6.75	0.54	0.53	0.29	3.50	1.35	4.85	29.0	27.9	0.7	39.8	32.8	0.69	40
			Bt1	31-72	7.5 YR 4/4	5.2	4.6	9.7	1.40	0.33	0.14	0.13	1.90	0.60	2.50	21.3	23.8	—	39.5	31.0	0.86	60
Esquina	164	Andic Humitropept	A	0-26	7.5 YR 3/4	4.3	3.7	8.0	11.93	0.79	0.92	0.42	4.10	2.13	6.23	42.6	34.2	1.7	45.9	29.8	0.66	31
			Bw1	54-117	7.5 YR 3/4	5.3	4.3	9.2	0.54	0.16	0.13	0.08	1.80	0.37	2.17	22.4	17.1	—	40.0	33.7	0.85	56
Valley bottom and swamp units																						
Surá-Saltito ^a		Typic Humitropept	A	0-19	10 YR 3/4	4.2	4.0	8.0	10.74	0.63	0.38	0.29	3.67	1.30	4.97	33.0	26.2	9.7	46.9	36.6	0.57	42
			Bw1	38-99	7.5 YR 4/4	4.9	4.4	9.6	2.06	0.52	0.19	0.08	2.17	0.79	2.96	23.1	26.7	—	42.4	32.5	0.84	64
Salto	165	Lithic Humitropept	A	0-12	10 YR 4/6	4.7	4.2	9.3	6.16	0.59	0.42	0.36	2.30	1.37	3.67	25.8	37.3	15.0	34.0	26.9	N.A.	19
			Bw	12-45	10 YR 4/8	5.3	4.5	9.7	1.81	0.18	0.21	0.12	1.20	0.51	1.71	19.0	29.8	—	34.0	28.4	N.A.	42
Taconazo	127	Typic Tropaquept	A	0-12	10 YR 4/2	4.4	4.1	9.3	3.02	1.30	0.79	0.36	2.50	2.45	4.95	32.4	49.5	3.6	52.9	45.7	0.44	11
			Bw1	12-22	7.5 YR 5/2	5.1	4.3	10.2	4.09	0.73	0.25	0.15	1.70	1.13	2.83	36.5	39.9	—	37.2	33.9	0.76	36
Piper	126	Typic Humitropept	A11	0-16	10 YR 3/3	5.2	4.7	9.8	9.38	11.50	2.67	0.71	0.50	14.88	15.38	38.6	96.7	6.4	45.2	32.6	0.72	4
			Bw1	35-108	10 YR 4/4	6.2	5.2	9.8	1.68	12.30	3.30	0.20	0.40	15.80	16.20	29.8	97.5	—	39.4	25.9	0.69	6
Peje	167	Typic Humitropept	A11	0-30	10 YR 3/3	5.5	4.6	9.5	5.70	8.00	3.92	0.71	0.50	12.63	13.13	35.0	96.2	7.4	49.3	30.9	0.82	10
			Bw	59-94	10 YR 4/3	6.0	5.0	9.5	1.21	11.40	3.86	0.13	0.30	15.39	15.69	33.0	98.1	—	44.1	29.0	0.74	20
Pantano	89	Histic Tropaquept	Ag	0-15	10 YR 3/1	4.9	4.2	9.5	10.36	1.98	0.71	0.51	1.60	3.20	4.80	37.1	66.7	—	56.1	34.7	N.A.	13
			Bg	15-100	10 YR 5/1	5.0	4.2	9.7	10.68	2.60	0.83	0.41	1.50	3.84	5.34	35.0	71.9	—	53.7	34.0	N.A.	23
Pantano	145	Typic Tropaquept	A	0-18	10 YR 3/2	4.9	4.3	8.8	7.64	3.38	1.67	0.56	1.10	5.61	6.71	29.2	83.6	—	43.4	30.8	0.45	33
			Bw1	18-55	10 YR 4/3	5.4	4.6	9.3	1.68	2.22	1.63	0.42	0.70	4.27	4.97	22.3	85.9	—	39.9	29.9	0.86	61
Units of the Río Sarapiquí terraces																						
Platanilla	119	Typic Tropopsamment	A	0-28	10 YR 3/2	5.3	5.2	9.4	4.89	11.25	2.84	1.73	0.30	15.82	16.12	25.3	98.1	4.7	31.0	17.6	0.84	4
Cacao	114	Fluventic "Andic" Eutropept	A	0-20	10 YR 3/2	6.2	5.2	9.7	5.36	13.00	2.54	0.92	0.20	16.46	16.66	23.0	98.8	—	37.5	26.2	0.81	5
			Bw	20-35	10 YR 3/3	6.9	5.4	9.9	0.74	9.25	2.04	1.89	0.30	13.18	13.48	18.8	97.8	—	42.1	10.1	0.89	10

Limonal ^a		Fluventic Eutropept/ Typic Tropopsamment/ Fluvaquentic Eutropept	A	0-10	10 YR 3/2	6.1	4.6	9.1	4.57	10.25	4.52	0.95	0.63	15.73	16.35	22.1	96.2	26.5	33.8	18.7	1.01	7
			Bw/	30-45	10 YR 3/3	6.4	4.8	9.4	1.01	9.52	3.68	0.33	0.70	13.53	14.23	20.6	95.1	—	28.0	19.0	1.10	9
Bambú	115	Andic Eutropept	A11	0-19	10 YR 3/3	6.6	5.6	10.2	2.55	4.43	1.58	2.30	0.40	8.31	8.71	31.7	95.4	0.2	43.7	32.6	0.76	10
Guayabal	116	Andic Dystropept	Bw1	29-95	10 YR 3/3	7.0	5.3	9.8	0.00	11.50	3.54	0.46	0.20	15.50	15.70	30.0	98.7	—	56.3	27.8	0.78	10
			A11	0-16	10 YR 3/3	4.6	4.3	9.1	6.63	1.15	0.63	0.41	1.00	2.19	3.19	19.2	68.7	1.4	37.7	31.2	0.83	25
Chanchera	113	Andic Dystropept	Bw	48-97	10 YR 3/4	5.6	5.2	9.8	0.27	0.90	0.21	0.10	0.20	1.21	1.41	17.1	85.8	—	53.1	43.4	0.71	54
			A	0-9	10 YR 3/3	4.3	—	8.4	7.71	1.10	0.88	0.46	3.60	2.44	6.04	24.2	40.4	7.9	45.6	40.5	0.82	22
Helechal ^a		Oxic Humitropept/ Oxic	Bw1	27-71	10 YR 4/3	4.9	4.1	9.9	0.94	0.75	0.21	0.26	3.80	1.22	5.02	26.5	24.3	—	39.8	27.4	0.67	45
			A	0-10	10 YR 3/4	4.3	3.9	8.7	9.15	0.50	0.27	0.18	2.72	0.96	3.68	29.3	26.0	—	39.8	33.0	0.76	38
		Dystropept	Bw1	10-32	10 YR 4/4	4.4	4.1	9.1	3.20	0.29	0.09	0.19	1.63	0.58	2.20	19.3	26.2	—	35.1	30.7	0.93	46
La Guaria	88	Fluventic Dystropept	A	0-22	10 YR 3/3	4.6	4.2	9.3	4.38	0.83	0.75	1.09	1.50	2.65	4.15	21.3	63.9	4.5	36.6	27.8	0.91	33
Units of the R. Puerto Viejo terraces																						
Puente	151	Typic Dystrandep	A11	0-21	10 YR 2/2	6.4	5.6	10.1	12.06	19.75	4.42	2.49	0.30	26.66	26.96	51.0	98.9	3.7	54.6	36.0	0.47	4
			Bw1	33-104	10 YR 4/3	6.6	5.0	10.1	1.68	4.34	3.29	0.35	0.30	7.98	8.28	34.0	96.4	—	62.6	33.4	0.76	19
Holdridge ^a		Andic Humitropept	A	0-22	10 YR 4/3	4.7	4.3	9.3	8.91	1.34	0.81	0.44	2.47	2.59	5.06	19.9	51.2	9.8	41.4	30.0	0.68	28
			Bw1	26-77	10 YR 4/4	5.3	4.5	10.0	1.50	0.62	0.40	0.16	1.87	1.18	3.05	23.2	38.8	—	37.4	27.3	0.76	40
Pejiballe	107	Typic Humitropept	A11	0-26	10 YR 3/3	4.7	4.3	9.6	6.27	1.03	0.46	0.36	1.60	1.85	3.45	19.6	53.6	0.6	43.6	34.9	0.65	30
			Bw1	43-94	10 YR 3/4	5.3	4.7	9.6	2.28	0.98	0.33	0.26	0.50	1.57	2.07	19.6	75.8	—	41.8	34.0	0.89	40
Experimental	112	Andic Humitropept	A11	0-15	10 YR 3/3	4.3	3.8	8.4	13.20	1.35	0.58	0.51	3.40	2.44	5.84	18.2	41.8	0.3	46.3	34.1	0.76	35
			Bw1	91-134	10 YR 3/4	4.9	4.2	9.8	0.00	1.00	0.38	0.46	2.20	1.84	4.04	18.6	45.5	—	34.4	28.1	0.95	50
Estación del Río	152	Typic Dystropept	A	0-15	10 YR 4/3	4.3	4.1	8.5	7.57	0.54	0.71	0.33	3.50	1.58	5.08	32.0	31.1	15.5	40.5	33.1	0.65	34
			Bw1	32-106	10 YR 4/4	5.1	4.2	9.5	0.60	0.32	0.25	0.09	3.00	0.66	3.66	22.0	18.0	—	37.8	29.4	0.90	54
Arboleda	128	Typic Humitropept	A	0-14	10 YR 4/3	5.3	4.9	8.9	4.03	11.00	2.96	0.41	0.40	14.37	14.77	34.9	97.3	1.5	42.4	33.9	0.55	6
			Bw1	14-93	10 YR 4/4	5.2	4.3	9.8	1.34	1.38	0.38	0.15	1.00	1.91	2.91	14.0	65.6	—	31.2	29.9	0.82	23

^aMean of multiple soil pits.

^bBase saturation = (sum of bases/ECEC) × 100.

^cAcid ammonium fluoride extraction.

soils of this area were described by Sancho and Mata (1987) but not mapped. A small area of Peje consociation lies within the Vargas annex and, thus, appears on the soil map (fig. 4.4). The Peje consociation is distinctive in that depth to the C horizon averages only about 90 cm. The dominant soil is a Typic Humitropept whose surface horizon is quite similar chemically to those of the Piper and Arboleda units. The A horizon is moderately acid, and base content is high. The B horizon of the Arboleda, however, is substantially more acidic and base-poor than that of either the Piper or Peje units.

The Pantano (swamp) complex is found in La Selva's swampy depressions. High water tables in such areas have caused reducing conditions, and OM has accumulated. The soils, all Tropaquepts, are typically gleyed and mottled. Three soil types recur regularly in a predictable but extremely complex pattern apparently unrelated to soil age or parent material. Histic Tropaquepts occupy areas where the water table is often above the soil surface and organic matter has accumulated in especially large amounts. Where the water table remains lower, soils are Typic Tropaquepts. Lithic Tropaquepts have formed wherever the streams have cut the valley floor down to the underlying bedrock. The three types form a similar, highly interdigitated pattern throughout the swampy portions of the property and were, thus, grouped as a complex by Sancho and Mata (1987) rather than mapped separately.

The Río Sarapiquí Terraces

The lower terraces along the Río Sarapiquí appear to have been formed as the river downcut through old alluvium. The new material was deposited atop the old during overbank flow. Currently, the river is downcutting mainly through the Tacónazo lava flow (and through buried soils derived from it). The Río Sarapiquí shows little evidence of meandering although one abandoned channel can be seen along the base of the Cerros Los Arrepentidos (see fig. 4.1).

The lowest terraces comprise an active floodplain with an exceedingly complex mosaic of soil types (fig. 4.5). All of the lowest terrace soils are base-rich with pHs in the 6's. The Pedregal (rocky land) consociation consists of skeletal soils (rich in coarse fragments) with no B horizon. The dominant soil is a Typic Tropofluvent. (It was originally designated a Fluventic Troporthent by Sancho and Mata [1987] on the assumption that the unweathered cobbles in the C horizon represented a lithic contact, but, in fact, a lithic contact must be continuous or nearly so [USDA Soil Survey Staff 1987]). Despite their highly skeletal nature, these soils support a forest of large stature, mainly in the vicinity of a gravel-mining operation that is steadily destroying it.

The Platanilla (*Heliconia* patch) consociation lies along the Río Sarapiquí on the western side of the Vargas annex (see fig. 4.5). Soils are sandy textured without gravel or rocks. The dominant soil type is a Typic Tropopsamment.

The Cacao (cocoa) consociation occupies mainly the now-abandoned cacao plantation at the junction of the Ríos Sarapiquí and Puerto Viejo (see fig. 4.5). A weakly developed cambic B horizon overlies a C horizon that shows striking discontinuities, evidence of repeated depositional cycles that may indicate alternation of flooding by the two rivers. Textures range from silt to sand; rocks and gravel are absent. Base content and pH are high as in all the lower-terrace soils. The

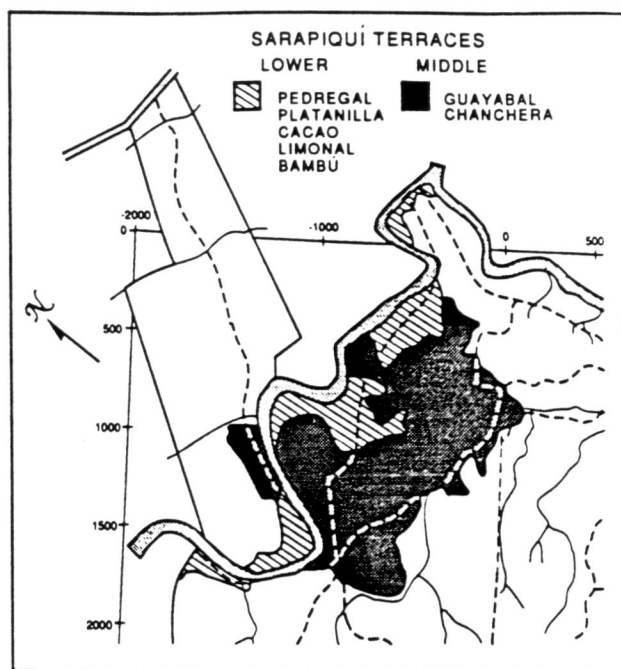


Fig. 4.5. Soils of the Río Sarapiquí lower terraces (Pedregal, Platanilla, Cacao, Limonal, and Bambú consociations) and middle terraces (Guayabal and Chanchera consociations).

dominant soil was designated a Fluventic "Andic" Eutropept by Sancho and Mata (1987) to emphasize its similarity to ash-derived soils.

The Limonal (grove of lime trees) consociation occupies the northern bank of the Río Sarapiquí at about 38- to 42-m elevation near the ford and cable crossing. Surface horizons, including a weakly developed (cambic) B, are sandy without gravel or rocks. A-horizon pH is only very slightly acid, and base-cation content is quite high (table 4.1). The C horizon shows evidence of distinct depositional events; in some areas stream-rounded cobbles are encountered at <1-m depth. The high sand content results in a bulk density that is unusually high by La Selva standards (1.0 g/cm^3) and which distinguishes the Limonal from the Cacao consociation. The major soil type was classified as a Fluventic Eutropept by Sancho and Mata (1987) but could equally well be designated an "Andic" Tropofluvent. The lower-terrace plots of Robertson and Sollins occupy about one-third of this mapping unit, and the four soil pits upon which the previous description is based lie immediately adjacent to these plots.

Soils of the Bambú (bamboo) consociation occur only on the Las Vegas Annex along the Río Sarapiquí. The soils appear to differ from the Limonal only in that the B horizons of the Bambú are better and more deeply developed. Surface soil pH is 6.6 with a high pH (10.2) in sodium fluoride and low bulk density even in the B horizon (0.76 g/cm^3). (The high NaF pH indicates the presence of large amounts of allophane [an amorphous gel-like clay mineral] or amorphous organo-alumino materials [USDA Soil Survey Staff 1987]. The low bulk density [$<0.85 \text{ g/cm}^3$], and pH [in water] >5 are corroborative.) The ECEC of this soil is quite low; however. Measured clay contents of 10% in the A and B horizons (table 4.1)

could be an artifact caused by the presence of allophane. The dominant soil is an Andic Eutropept.

The middle terraces of the Río Sarapiquí have not flooded in recent memory; thus, these soils, although still quite fertile, are more deeply and extensively weathered than those of the lowest terrace. The Guayabal (guava grove) consociation lies on level terrain in the Sarapiquí Annex and is traversed by the Atajo and Las Vegas trails. Surface soil is moderately acid, and base content is moderate. A C horizon consisting of compacted alluvial sand underlies a deeply developed (cambic) B. A buried alluvial soil is encountered at about a 2-m depth. The dominant soil is an Andic Dystropept.

The Chanchera (pig barn) consociation occupies gently undulating land in the Sarapiquí Annex and is traversed by a trail of the same name. The surface Chanchera soil is more acid and base-poor than the Guayabal but still classifies as an Andic Dystropept. The B horizon is deep and well developed but contains abundant volcanic rocks in various stages of weathering.

The Helechal (fern patch) consociation occupies the highest terrace within the La Guaria Annex (fig. 4.6) and is the site of the upper-terrace plots of Robertson and Sollins. Relief is gently undulating; hills that protrude from this unit, especially near the Río Sarapiquí, create islands of much older soil (mapped currently as Matabuey). The following information is based on four pits, located adjacent to the Robertson-Sollins plots, that were described and sampled by Sancho and Mata in 1989. The Helechal surface soil (0.15 cm) is strongly acid (pH 4.4) and extremely base-poor (only 1.0 cmol (+)/kg total bases). Sodium fluoride pH is between 8.7 and 9.4, and bulk density is $<0.85 \text{ g/cm}^3$ throughout the top 1 m of profile. Levels of oxalate-extractable aluminum and iron are too low to meet the new definitions of Andic subgroups (USDA Soil

Survey Staff 1987). All four profiles meet the requirements for Oxyc subgroups, based on clay contents calculated as 2.5 times moisture contents at -1.5 MPa . The soils classify, therefore, as Oxyc Dystropepts or Oxyc Humitropepts depending on organic matter content, which is highly variable ($7\text{--}15 \text{ kg C/m}^2$ to a 1-m depth). A 2-ha portion of what was mapped originally by Sancho and Mata as Helechal consociation, lying to the south of the small stream that crosses Ave. Marañon (see fig. 4.5), is a relatively unweathered soil that classified as a Typic Hapludand upon further sampling in 1989 (F. Sancho and R. Mata unpublished data).

Described by Sancho and Mata (1987) as occupying a middle terrace, the Helechal, in fact, constitutes the uppermost terrace of the Río Sarapiquí. A topographic survey along Ave. Marañon and in the vicinity of the Robertson/Sollins plots shows that the Helechal unit ranges in elevation from 46 to 52 m, and lies some 1 to 10 m higher than the La Guaria consociation (described next). The sequence of deposits in which the Helechal soils have formed can be seen well in a roadcut along Ave. Marañon between locations 1000/–1340 and 1100/–1320 on the La Selva grid. Here a fine-textured surface deposit about 1-m thick, from which the Helechal surface soil derives, overlies a weakly cemented, well-weathered sand, which overlies, in turn, a buried profile developed from Taconazo lava. The cemented sand occurs at depth throughout the lower parts of the Río Sarapiquí valley and may represent the lahar (volcanic mud flow) from which the La Guaria soils have formed (described next). At least some of the Helechal soils (along with the La Guaria, described next) appear to have been used for mechanized rice production for about three years around 1960. Their extreme infertility may result in part from this land-use history in addition to natural processes of soil development.

The La Guaria (nearby bar and settlement named, in turn, after the national orchid of Costa Rica) is unique among La Selva's soils in that it derives from a lahar rather than an alluvial deposit or lava flow. Its exact age is unknown, but the lahar appears to be older than the upper-terrace deposits of the Río Sarapiquí but younger than the Taconazo lava. Angular to subangular well-weathered rocks of diverse composition are found embedded in a clay matrix in the subsoil at many locations; the angularity of the rocks indicates that they were deposited as a lahar rather than as alluvium, and their diverse composition rules out the possibility that they derive from a lava flow. Interestingly, the La Guaria land surface is lower than the Helechal, even though the latter is nearer the present river course, suggesting a depositional history that is, at the very least, complex.

La Guaria soils occupy nearly level land between the Helechal unit and the main road to Puerto Viejo (see fig. 4.6). Surface soil pH averaged 4.6, and bases summed to 2.5 cmol (+)/kg . The La Guaria consociation was classified as a Fluventic Dystropept by Sancho and Mata (1987) because organic matter content varied somewhat irregularly with depth and because a buried soil was found at 1.7-m depth in one of the two pits. Subsequent field work suggests that this pit was located in an area where Helechal soils lie atop the lahar, in which case the La Guaria soils will need to be reclassified. The Canadian forestry trials and nearby Nelder plots (chap. 24) are located on this unit, as is one set of TRIALS plantings.

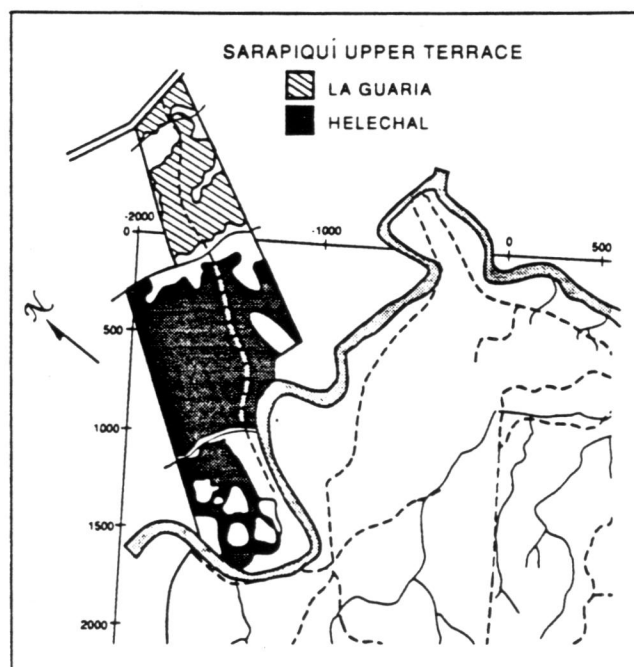


Fig. 4.6. Soils of the Río Sarapiquí upper terraces (Helechal and La Guaria consociations).

The Río Puerto Viejo Terraces

The Río Puerto Viejo has a gentler gradient than the Río Sarapiquí; thus, it has meandered more and deposited finer materials. At least four major terraces are evident near La Selva, of which only the lowest floods currently.

The Puente (bridge) consociation occupies generally flat land at about 29-m elevation near the mouths of the Quebradas Surá, Salto, Sábalo (fig. 4.7). Excellent profiles can be seen at the swimming hole below the bridge over the Quebrada El Salto. The entire profile is stone free but light textured. The high pHs in water and NaF (6.4 and 10.1) and low bulk density (0.47 g/cm^3) of the A horizon suggest the presence of substantial amounts of allophane. A cambic B horizon with mottling extends below 1-m depth, suggesting moderately poor drainage. The major soil type is a Typic Dystrandept; inclusions are mainly Aquic Dystrandepts. Low-lying areas along the Quebrada El Surá between the River Station and the laboratory complex, and extending upstream into the arboretum are currently assigned to this unit purely on the basis of elevation.

The Sainal (a semi-invented word meaning area frequented by sains, pigs or peccaries) consociation, as presently recognized, includes the level area bounded by the Cacao consociation to the west and extending east to the slope break at about 120 m on the Sendero Occidental. The terrace lies at about 36 m elevation and floods at least occasionally. This consociation was not described or sampled by Sancho and Mata (1987); their pit no. 107, labeled La Selva soil, is located instead within the Pejiballe consociation discussed later. (We have chosen not to use the name La Selva for any map unit to avoid difficulties in distinguishing between a soil from somewhere at La Selva and a soil from a specific map unit named La Selva.) The only chemical data for the Sainal soils come from augered surface soil samples that gave a mean value for extractable phosphorus of $14.2 \mu\text{g/g}$.

The Holdridge (trail named for Leslie Holdridge, founder of Finca La Selva) consociation occupies flat to gently undulating land on a middle terrace (36- to 38-m elevation) to the north and west of Quebrada Esquina (see fig. 4.7). Whether this and the Sainal mapping unit flood regularly is uncertain; both, however, did flood in 1970 (V. Chavarría pers. comm.). Soils are stone free and moderately weathered with intermediate acidity and base saturation. The Río Puerto Viejo cuts through soils of this unit at Rafael's point, exposing many layers of alluvium. Below these, beginning about 1 m above the dry-season water level, is a buried, highly weathered soil grading downward into Taconazo saprolite. The successional strips, OTS plots 4 and 5, and the well-drained portion of OTS plot 2 (M. Lieberman et al. 1985) are all on this mapping unit as are sites sampled by Robertson (1984), Sollins et al. (1984) and Werner (1984). The dominant soil is an Andic Humitropept.

The Pejiballe (a palm that produces edible fruit and heart) consociation occupies a middle terrace at about 42-m elevation in the general vicinity of the laboratories and researcher cabins. This terrace has not flooded in historic times (I. Alvarado and V. Chavarría pers. comm.). Soils near the dining hall and other facilities across the river may belong to this consociation because they appear to be at the same elevation. A 10-m profile showing many depositional layers is kept continually exposed near the directors' house as the area is undercut

steadily by the Río Puerto Viejo. The surface soil is well drained and stone free with an A horizon that is strongly acid, base poor, and OM rich. Soils of this unit are less weathered than those of the Experimental, which it adjoins. It is similar to the Helechal and La Guaria on the Río Sarapiquí terraces but richer in OM and base metal cations. The dominant soil is a Typic Humitropept.

The Experimental (name of trail) consociation occupies undulating and moderately dissected upper-terrace land (40- to 50-m elevation) lying mainly to the northeast of the Quebrada El Surá. This unit occupies terrain more dissected than does the Helechal or La Guaria unit along the Río Sarapiquí or the Estación del Río farther upstream along the Río Puerto Viejo. Chemically, however, all these upper-terrace soils are similar. The dominant soil is an Andic Humitropept; inclusions are mainly Andic Dystropepts. The well-drained portions of OTS plot 1 (M. Lieberman et al. 1985) are located on this map unit.

The Estación del Río consociation (river station) occupies a small, gently undulating portion of the upper terrace at the site of the old field station and the Reserva Ecológica Rafael Chavarría (see fig. 4.7). The dominant soil is a Typic Dystropept.

The Arboleda (arboretum, in local usage) consociation forms a band of strongly undulating land just downslope from the Jaguar unit in the general vicinity of the Quebrada Arboleda (see fig. 4.3). The origin of the soils of this unit has been debated for several years. Although long viewed as lying well above the uppermost alluvial terrace and, thus, necessarily residual, these soils lack clay skins in the B horizon and are substantially less acid (pH 5.3 in the A horizon) and more base rich than the Jaguar or Matabuey soils. It now seems clear that this consociation occupies a very old river terrace, now so thoroughly dissected that it is barely recognizable as such. This reappraisal is based on the following reasoning. The highest parts of the Arboleda unit appear to correspond in elevation to the uppermost land surface to the north of the La Selva station along the main road between Puerto Viejo and Río Frío; cuts made through this surface during road relocation in 1989 revealed it as an old alluvial terrace now highly dissected. In addition well-weathered stream-rounded pebbles can be found exposed on trails to about 60 m elevation in numerous parts of what was mapped originally as Arboleda soils and in other parts of the property. The dominant soil of the Arboleda consociation was classified tentatively as a Typic Humitropept by Sancho and Mata (1987) because auger samples showed consistently dark colors, which suggest high OM levels. In fact, OM levels in the single soil pit sampled were fairly low (7.5 kg C/m^2); thus, additional sampling is needed to classify these soils definitively.

Bioassays by Denslow et al. (1987) that show slight growth response to phosphorus and cations but not to nitrogen used an Arboleda soil. Of the natural tree-fall gaps studied by Vitousek and Denslow (1986), numbers 4 and 7 were on Arboleda soils; the rest were on Jaguar. OTS plot 3 (M. Lieberman et al. 1985) is located on this map unit.

Major Unresolved Issues

Although work summarized here has given the first comprehensive picture of La Selva's soils, it raises yet new questions

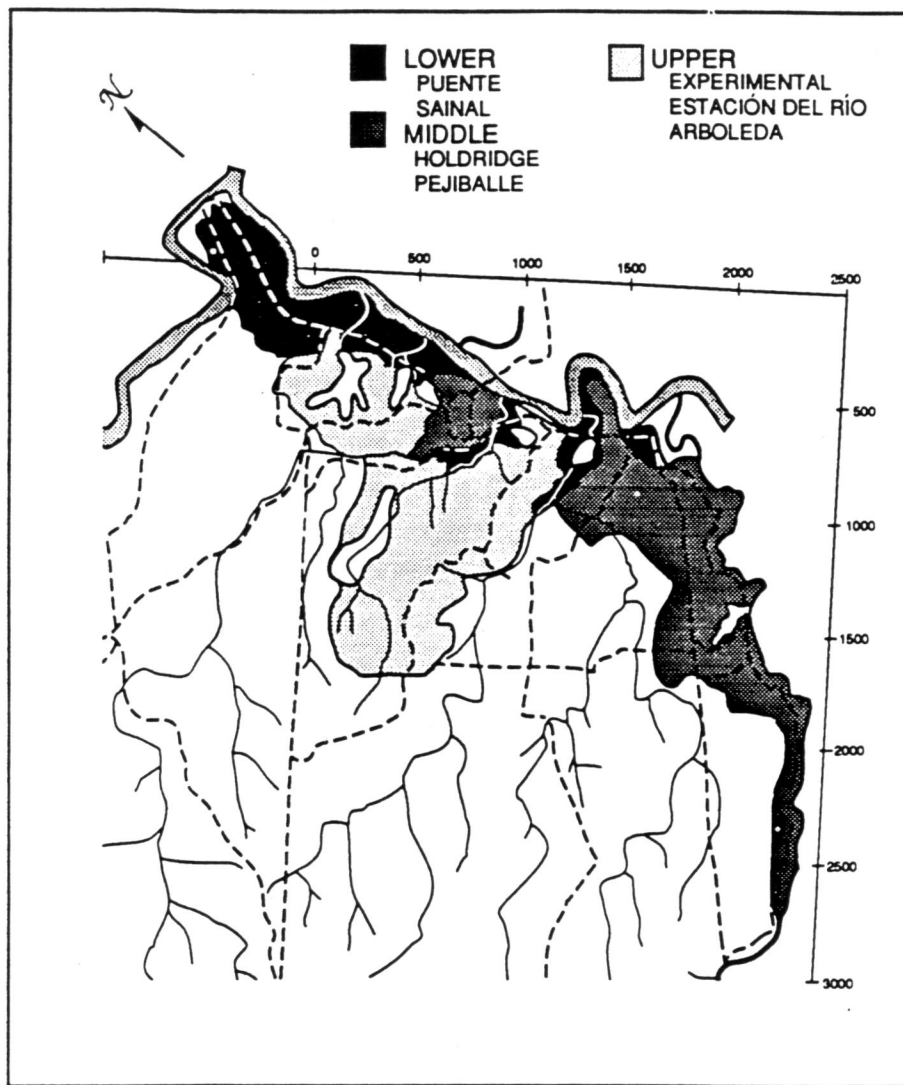


Fig. 4.7. Soils of the Río Puerto Viejo terraces: lower (Puente and Sainal consociations), middle (Holdridge and Pejiballe consociations), and upper (Experimental, Estación del Río, and Arboleda consociations).

about their genesis and classification. The age of these soils remains unknown. We really have no idea of the time it has taken a parent material of a given texture to weather to its current state in the warm, moist environment at La Selva.

The influence of parent material on the nature of La Selva's residual soils remains poorly understood. Vitousek and Den-slow (1987) felt that the Esquina and Salto lavas have given rise to soils of different color and phosphorus availability. Sancho and Mata (1987), however, found few chemical and morphological differences between any of the residual soils. It must be noted that the geological survey of Alvarado (1985) is preliminary; thus, the boundary between Salto and Esquina lava must be regarded as tentative. Better mapping of the lava flows might yet show the corresponding soils to be quite different.

The correspondence between lava flow and soil type in the current mapping is further confused in that the Matabuey soils have developed in two rather different lava flows. Originally, Sancho and Mata (1987) described the Matabuey unit as developed solely from Salto lava. Subsequent field work has shown that, in the hilly areas immediately adjacent to the Río Sarapiquí including much of the La Guaria Annex and adjoin-

ing farms, the soils presently regarded as Matabuey consociation have developed from Taconazo lava, readily identifiable by the presence of large (>1 cm) feldspar crystals. (For example, a trench extending uphill from the parking area at the end of Ave. Marañon [1440.-1160 on the La Selva grid] uncovered Taconazo saprolite to about a 54-m elevation but revealed no sign of Salto lava overlying Taconazo.) Despite the difference in parent material, Sancho and Mata's data show no difference in chemistry or morphology between the two portions of the Matabuey unit.

The current mapping of hilly areas adjacent to the Río Sarapiquí is questionable. At present the hills are mapped as Matabuey and the surrounding areas as Helechal. In fact, the degree of soil development increases steadily as one moves upward toward the crests of these hills, presumably because the upslope positions are more stable. (For example, a trench at grid location 1440/-1160 in the La Guaria Annex showed that the B horizon increases in thickness from 40 cm to >3 m and is increasingly reddish as one proceeds uphill. Numbers and size of iron nodules increase also.) Nonetheless, stream-rounded stones with obvious weathering rinds are found in the upper 50 cm of the profile, even at the tops of the highest hills

(e.g., at a 60-m elevation throughout the adjoining property immediately southwest of the La Guaria Annex). Apparently, alluvium at one time covered this entire landscape then was removed to varying depths by fluvial and colluvial processes. At present, soils at the highest points are largely residual in origin, but those at lower positions on the landscape derive from some indeterminate mixture of residuum and old alluvium. Indeed, in some places highly weathered soil has moved downslope and now lies atop very young alluvium (e.g., location 1360, -1300 in the La Guaria Annex). Quite possibly the entire hilly area along the Río Sarapiquí (and, perhaps, the area south of the Río Puerto Viejo now mapped as Arboleda) would be mapped best as a complex.

Finally, the origin of the lahar that forms the parent material for the La Guaria soils and underlies at least portions of the Helechal consociation represents a major mystery. Given its degree of weathering, stratigraphic position, and position in the landscape, it seems possible that the lahar descended from the Cerros Los Arrepentidos rather than from the volcanoes of the cordillera, after the first of the lava flows that formed the landscape of Old La Selva but, clearly, well before the current cycle of deposition and downcutting by the Río Sarapiquí. Substantial field and laboratory work will be needed, however, to document fully its extent and origin.

SOILS PROCESS RESEARCH AT LA SELVA

Mineralogy

The mineralogy of a soil—that is, the nature and amount of clay-size mineral particles—is, perhaps, the single best correlate of its genesis, fertility, and physical structure. Unfortunately, mineralogy has been little studied at La Selva.

For the lower- and some middle-terrace soils (table 4.1), high pHs in sodium fluoride suggest the presence of allophane as an early weathering product of the volcanic parent materials. Werner (1984) described La Selva's soils as dominated by allophane, kaolinite (a weathered layer-silicate clay) and halloysite (a precursor of kaolinite) with quartz and gibbsite (aluminum hydroxide) present in similar, but presumably small, amounts. In fact, Werner's work dealt only with a middle-terrace consociation (Holdridge) and so agrees with current understanding.

For the one upper-terrace soil studied to date (Helechal at 0–15 cm depth), X-ray diffraction patterns indicate the presence of kaolinite, halloysite, and gibbsite (J. Borchers and J. Baham, Oregon State University, unpublished data). To see these patterns, it was necessary to remove iron sesquioxides, which precluded detection of goethite (a common iron oxide). Citrate/dithionite extractable iron averaged 10.5% (SE = 0.3%) in surface soil (0–10 cm depth) from this unit, however, suggesting a substantial accumulation of goethite (P. Sollins unpublished data).

On the basis of these admittedly meager data and patterns observed for volcanic soils elsewhere in the world, one can expect a certain weathering sequence at La Selva. Allophane should be abundant at early stages, converting later to halloysite, then to kaolinite, and lastly to gibbsite. Goethite should accumulate in large amounts throughout the weathering process. Some small amount of 2:1 layer-silicate clays must be

present even in the most weathered La Selva soils to account for the fairly high levels of potassium chloride-exchangeable aluminum. It should be noted that most of these minerals are predominantly variable-charge; that is, the cation and anion exchange capacity (CEC and AEC) are affected strongly by the pH and ionic strength of the soil solution (Uehara and Gillman 1981; Sollins et al. 1988).

Physical Structure and Hydrology

Soil physical structure is important because it affects water-holding capacity (thus, plant growth), rates and pathways of water infiltration (thus, erosion and nutrient movement), and aeration and microbial activity (thus, turnover and transformations of carbon and nitrogen). The physical characteristics of La Selva soils are unusual and reflect their volcanic origin.

To compare La Selva soils with others, we used data provided by the USDA Soil Survey Staff (1975), selecting soils for which the temperature was isomesic or isothermic and the moisture regime was udic or perudic (table 4.2). Although most of the soils were from Puerto Rico and Hawaii, they may be fairly representative of the tropics because they were chosen by the Soil Survey Staff to represent a wide range of soil types. Comparison with a wider range of soil would be preferable but was not possible with the resources available.

As mentioned, La Selva's soils reflect their volcanic origin by their physical characteristics. Bulk density, for example, averages lower at La Selva than elsewhere (fig. 4.8a). Water-holding capacity (at -1.5 MPa) averages higher in La Selva soils, reflecting a somewhat different pore-size distribution than in soils elsewhere. Clay content tends to be lower at La Selva (fig. 4.8b), but the low clay content probably reflects the difficulty in dispersing the clay rather than any lack of clay per se. Although unusual by world standards, such physical characteristics are typical of volcanic soils (e.g., Warkentin and Maeda 1980; Sollins et al. 1983; Spycher et al. 1983; Russel and Ewel 1985).

Within La Selva, however, soil physical structure varies greatly. The weathered soils, such as the Ultisols Matabuey, Jaguar and the more weathered Inceptisols (e.g., La Guaria, Helechal, Experimental, and Arboleda), have excellent structure. Because the soils are clay rich, fine pores are abundant and the soils retain large amounts of plant-available water. The clay is strongly microaggregated, however, with numerous large pores between the microaggregates. Water infiltrates readily into the soils through these large pores and drains freely. Thus, because of microaggregation, these soils behave like sandy soils in that they drain freely yet like clay soils in that they retain large amounts of plant-available water.

At La Selva, aggregation has been studied explicitly only on the Helechal consociation. Strickland et al. (1988) compared aggregation and aggregate stability of the dominant Helechal soil with that of five U.S. soils and found that the Helechal was the most extensively and stably aggregated. At least three factors could contribute to the extremely stable aggregation. Given the mineralogy of this consociation, binding by iron and aluminum oxides and hydrous oxides is probably important (see Tisdall and Oades 1982). Charge density is low because the soil pH is near the point of zero charge; thus, there is little tendency for the clay particles to repel one another (cf. Sollins et al. 1988). Last, the high OM content of the Helechal

Table 4.2 Chemical and physical properties of tropical soils worldwide.

Classification	Location	Land Use or Vegetation Type	Horizon	Depth (cm)	pH		Delta pH (H ₂ O-KCl)	Organic carbon (%)					Sum of Bases	CEC (NH ₄ OAc)	Water content (-1.5 MPa) (% by weight)	Bulk density (Mg/m ³)	Clay (%)
					H ₂ O	KCl			K	Ca	Mg						
												(cmol(+) /kg)					
Typic Acrustox	Brazil	Secondary forest	A1	0-10	5.0	4.2	0.8	3.24	0.15	0.42	0.32	0.91	15.0	24.0	—	71.6	
			B1	30-65	5.0	4.7	0.3	1.35	0.01	0.02	0.02	0.06	6.0	24.1	—	72.3	
Tropeptic Haplothox	Puerto Rico	Pasture	Ap	0-15	5.6	5.0	0.6	4.30	0.90	8.30	1.50	10.80	20.5	31.9	0.96	77.1	
			B21	15-33	4.7	4.6	0.1	1.75	0.50	1.80	0.20	2.50	10.6	33.6	1.07	76.8	
Aeric Tropaqualf	Puerto Rico	Pasture	Ap	0-18	4.6	4.0	0.6	1.48	0.10	9.40	3.00	12.80	20.7	21.7	1.20	40.5	
			B21t	30-43	4.8	3.5	1.3	0.54	0.10	5.10	4.40	10.30	18.5	22.9	1.29	48.4	
Oxic Dystrandept	Maui	Pasture	Ap	0-20	6.2	5.4	0.8	8.87	1.70	17.50	6.30	25.80	53.7	41.0	0.70	—	
			B21	20-41	6.6	5.8	0.8	3.51	1.80	11.80	5.40	19.00	40.6	49.1	0.70	—	
Typic Eutrandept	Maui	Cultivation	Ap	0-23	6.7	5.8	0.9	5.81	6.10	35.80	11.70	54.00	61.1	35.2	0.87	23.7	
			B2	41-63	7.4	6.4	1.0	2.58	0.30	42.70	12.30	61.30	63.1	43.2	0.76	13.9	
Typic Hydrandept	Hawaii	Old field?	Ap	0-18	5.4	4.5	0.9	11.70	0.50	9.40	2.60	12.80	53.1	101.9	0.51	—	
			B21	18-36	5.2	4.5	0.7	6.55	0.20	0.80	0.30	1.50	33.7	154.5	0.33	—	
Typic Vitrandept	Hawaii	?	A1	0-10	6.6	5.5	1.1	5.27	1.30	7.50	1.90	10.90	27.5	19.4	0.78	—	
			B2	10-20	6.5	5.6	0.9	2.12	0.30	1.70	0.30	2.40	18.6	23.7	0.75	—	
Typic Dystrorpept	Puerto Rico	Old field?	Ap	0-15	4.2	3.5	0.7	2.28	0.30	1.60	0.70	2.60	18.7	22.7	1.20	40.2	
			B	15-33	4.6	3.7	0.9	1.35	0.10	3.00	0.70	3.80	16.6	22.9	1.11	38.0	
Typic Eutropept	Puerto Rico	Old field?	Ap2	3-15	5.0	3.7	1.3	1.77	0.40	13.20	9.40	23.20	35.0	22.5	1.26	32.0	
			B	15-33	5.0	3.6	1.4	0.73	0.20	14.60	13.20	28.40	38.2	19.8	1.17	21.3	
Typic Acrorthox	Mayaguez, PR	Old field?	A1	0-28	5.1	4.3	0.8	6.04	0.10	1.30	0.10	2.90	25.4	26.5	1.08	54.5	
			B1	28-46	5.0	4.4	0.6	2.04	0.00	0.10	0.00	0.10	12.1	22.8	1.18	57.7	
Haplic Acrorthox	Belem, Brazil	Evergreen tropical forest	A1	0-4	4.1	3.5	0.6	2.76	0.08	0.07	0.09	0.27	6.7	13.1	—	34.7	
			B21	19-87	4.7	4.2	0.5	0.58	0.01	0.01	0.01	0.05	2.8	20.8	—	64.2	

Table 4.2 (continued)

Classification	Location	Land Use or Vegetation Type	Horizon	Depth (cm)	pH		Delta pH (H ₂ O-KCl)	Organic carbon (%)					Sum of Bases	CEC (NH ₄ OAc)	Water content (–1.5 MPa) (% by weight)	Bulk density (Mg/m ³)	Clay (%)
					H ₂ O	KCl			K	Ca	Mg						
												(cmol(+) /kg)					
Tropeptic Eutrothox	Vega Alta, PR	Pasture	Ap	0–20	5.6	4.9	0.7	2.73	0.60	8.10	2.10	10.90	15.1	26.7	1.22	73.1	
			B2t	20–46	5.4	4.7	0.7	0.94	0.60	4.20	1.60	6.50	9.5	30.1	1.25	81.2	
Typic Gibbsiorthox	Kauai	Pasture	Ap1	0–38	5.2	4.2	1.0	3.88	0.10	0.50	0.60	1.30	14.6	30.9	1.12	—	
			B2t	48–76	5.0	5.1	–0.1	1.58	0.00	0.00	0.60	0.60	4.8	33.4	1.12	—	
Tropeptic Umbriorthox	Kauai	Pasture	Ap	0–23	5.9	4.9	1.0	4.39	0.80	2.20	2.00	5.20	19.8	34.2	0.91	—	
			B2t	23–53	5.4	5.4	0.0	1.72	0.20	1.00	0.60	2.00	9.4	40.3	0.92	—	
Typic Torrox	Honolulu, HI	Cultivated	Ap1	0–15	5.7	5.0	0.7	1.92	0.40	6.00	3.00	9.70	—	22.3	—	—	
			B2t	38–66	6.4	5.8	0.6	0.50	0.00	3.00	2.20	5.80	—	22.1	—	—	
Oxic Plinthaquult	Toa Baja, PR	Cultivated	Ap	0–25	4.2	3.5	0.7	3.25	0.20	1.10	0.60	2.00	14.2	25.6	1.19	55.7	
			B1t	25–33	4.2	3.2	1.0	1.18	0.10	2.60	0.40	3.20	12.7	32.2	1.29	76.4	
Typic Tropohumult	Barranquitas, PR	Pasture	Ap	0–15	4.6	3.6	1.0	5.20	0.50	2.40	3.10	6.00	23.6	29.8	0.90	67.2	
			B2t	15–28	4.5	3.5	1.0	2.01	0.10	0.10	1.90	2.10	19.9	34.1	1.02	81.8	
Typic Tropudult	Puerto Rico	Pasture	Ap	0–15	4.7	3.7	0.0	2.40	1.60	2.10	0.90	4.70	14.1	20.7	—	47.9	
			B2t	15–41	4.6	3.4	1.2	0.67	0.50	0.10	0.50	1.10	12.8	23.7	—	55.1	
Aquentic Chromudert	Gurabo, PR	Orchard	Ap	0–18	4.8	4.0	0.8	1.96	0.40	5.80	11.00	17.60	25.5	22.4	1.20	47.7	
			A12	18–38	5.3	4.4	0.9	1.17	0.20	9.90	17.10	28.20	26.9	26.1	1.15	61.4	
Udic Chromustert	Lajas, PR	Old field	Ap	0–18	5.8	—	—	1.64	0.50	23.30	16.40	40.50	41.7	20.4	1.36	51.6	
			A12	18–36	5.9	—	—	1.29	0.50	23.60	17.50	42.10	41.2	23.5	1.41	55.0	

Source: All data based on compilation by USDA Soil Survey Staff (1975).

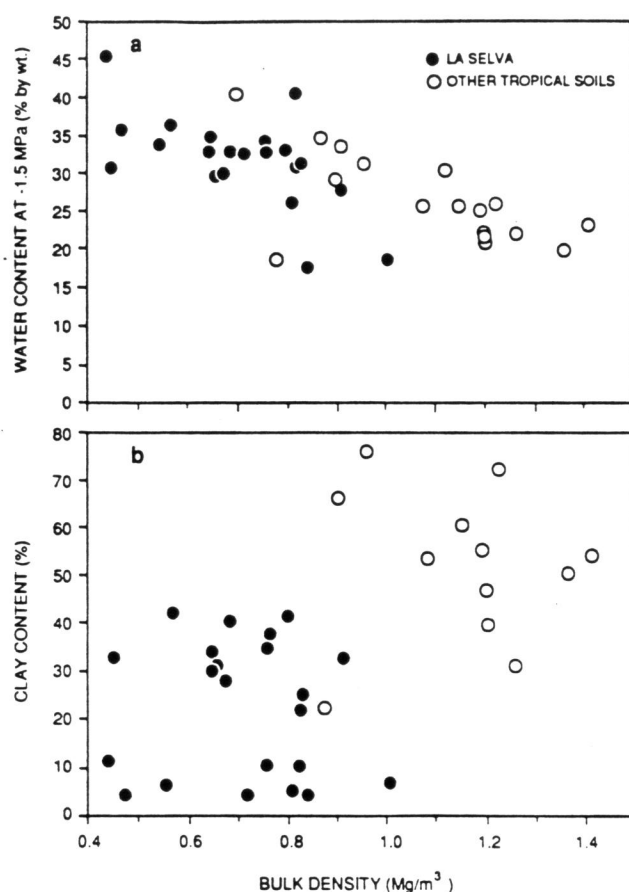


Fig. 4.8. Physical properties of La Selva soils and of other humid tropical soils. La Selva data are from table 4.1; data for other tropical soils taken from compilation by USDA Soil Survey Staff (1975); see text: (1) water-holding capacity at -1.5 MPa matric potential (dry weight basis) compared to bulk density; (2) clay content compared to bulk density.

is probably important, but this could be both a cause and an effect of the stable aggregation. Binding by allophane is probably important in the less-weathered soils at La Selva, but this has not yet been documented.

Because of strong aggregation, the texture of La Selva soils can be exceedingly difficult to measure. For example, field-moist Helechal surface soil shaken in sodium hexametaphosphate solution gave a clay content of 73% (Strickland et al. 1988), whereas air-dried Helechal soil treated similarly yielded a clay content of only 38% (table 4.1). Sollins (1989) confirmed that air-drying of Helechal soil caused nearly irreversible aggregation of clay-sized particles.

Aggregation alters water flow through the soil by creating large pores (macropores) between the aggregates. Root decay also creates macropores as does the activity of soil animals. Dye-staining patterns for the Helechal soil give visual evidence of the extensive macropore network (Sollins and Radulovich 1988). A more quantitative technique (Radulovich et al. 1989) showed that, of the total porosity of $0.62 \text{ m}^3/\text{m}^3$, about 13% was the result of macropores (those pores draining between 0 and -3 kPa).

Macroporosity affects rates of nutrient leaching. To the extent that water flows through the macropores and bypasses the micropores of the soil matrix, the nutrients already in the soil

matrix tend not to leach, and nutrients in litter leachate and throughfall tend not to enter the soil matrix (White 1985; Sollins 1989). Solute exchange between the rapidly moving bypass flow and the relatively immobile micropore water within the soil matrix was studied on the Helechal consociation by Sollins and Radulovich (1988). Solute breakthrough curves showed that more than two pore volumes of CaCl_2 solution must flow through the soil before CaCl_2 stops diffusing into the fine pores. This result implies that equally large volumes are needed to leach nutrients from the fine pores. McVoy (1985) and Seyfried and Rao (1987), working with a less-weathered Typic Dystropept under forest at Turrialba, Costa Rica, reported a similar, although somewhat less-pronounced, tendency for the soil to resist solute entry and leaching.

Measuring leaching rates is problematic in soil in which water drains mainly through macropores rather than through the soil matrix. Tension (porous-cup) lysimeters sample mainly the matrix water and give no indication of flow volumes; large zero-tension lysimeters collect the water actually draining the profile but are notoriously unreliable. Radulovich and Sollins (1987) improved water-collection efficiency of zero-tension lysimeters in the Helechal soil by using very large lysimeters and by pressing their rims upward into the soil, thus creating a saturated zone that promoted drainage into the lysimeter.

Because water drains rapidly through the macropores, it infiltrates readily into the soil instead of ponding on the soil surface or running off. On the Helechal soil, for example, initial infiltration rates averaged $3,900 \text{ mm/hr}$ although they were highly variable (Radulovich and Sollins 1985). Erosion rates are, thus, low except on steep slopes and on trails where foot traffic has compacted the soils. The structure of this soil can be damaged, however; light foot traffic, for example, compacted the Helechal soil enough to decrease penetrability by 50%-70% (Radulovich and Sollins 1985). The lower-terrace soils contain less clay (table 4.1) and appear to have a less stable structure; lower-terrace sites maintained vegetation-free for several years have undergone considerable erosion (P. Sollins and G. P. Robertson, unpublished data).

Charge Chemistry, CEC and pH

As mentioned, La Selva's soils are rich in variable-charge constituents (certain clay minerals and organic matter) whose CEC and AEC depend on the pH and ionic strength of the soil solution (see Uehara and Gillman 1981; Sollins et al. 1988). Some indication of this effect can be seen by plotting actual CEC (calculated as the sum of exchangeable bases plus exchangeable acidity) against CEC as measured with ammonium acetate (1 M) at pH 7. Although the two measures correlate (fig. 4.9), the ammonium acetate method consistently overestimates actual CEC, sometimes by a factor of 6. There are two reasons: (1) CEC increases with pH and is, thus, much higher at pH 7 than at actual soil pH; (2) CEC increases with ionic strength and is, therefore, much higher in a 1 M solution than in the actual soil solution (about 10^{-3} for the Helechal soil; Sollins and Radulovich 1988). This striking effect of measurement technique on the value of a critical soil parameter should serve as a warning that the limitations of techniques must be understood when discussing results of soils

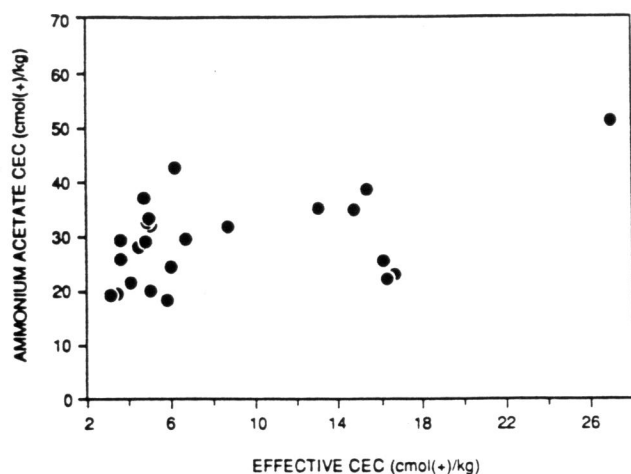


Fig. 4.9. CEC of La Selva soils as measured with molar ammonium acetate at pH 7 relative to actual CEC (sum of base plus acid cations). Data from table 4.1.

analyses, and that, in any case, methods must always be described carefully.

In terms of pH and cation levels, La Selva's soils can be grouped into two categories: Those with pH < 5 tend to have low levels of exchangeable base-metal cations (K, Ca, Mg) and high levels of exchangeable acid-metal cations (H^+ and Al); those with pH > 5 are more base rich and have lower levels of exchangeable acidity (fig. 4.10). Sum of bases and base saturation both increase with pH, but base saturation levels off at 100% above pH 5.0, which is to be expected because levels of exchangeable Al tend to be very low in the less-acid soils (fig. 4.10). La Selva's most base-poor soils (Helechal, Jaguar, and Matabuey) average 1.0–1.4 cmol (+)/kg in the A horizon (table 4.1), well above the lowest values reported elsewhere (table 4.2, see also the compilation by Lopes 1984). Whether cation levels influence productivity at La Selva is an important but unresolved question (see chap. 5).

CEC and pH are linked intimately in variable-charge soils (fig. 4.11): if pH changes seasonally or in response to management, so will CEC. Soil pH varies because of shifts in the balance between rates of processes that generate H^+ (sources) and rates of those that consume it (sinks). The major H^+ sources are plant nutrient uptake, root respiration, decomposition of organic matter to CO_2 and organic acids, and nitrification: weathering of soil minerals provides the largest H^+ sink although denitrification and nutrient release during decomposition can also be important (Van Breemen et al. 1983; Binkley and Richter 1987). There are limits to the extent that pH can shift because weathering (the major H^+ sink) proceeds at a rate roughly proportional to H^+ concentration in solution. Thus, for example, as pH drops because of increased nitrification, the higher H^+ concentrations cause weathering reactions to speed up, thereby increasing the rate at which H^+ is consumed.

Work on the Helechal consociation illustrates some of the large shifts in pH that can occur in response to disturbance. Ammonification rates are high in this nitrogen-rich soil, but vegetation takes up large proportions of this ammonium, and only a small fraction is nitrified. When plots were kept

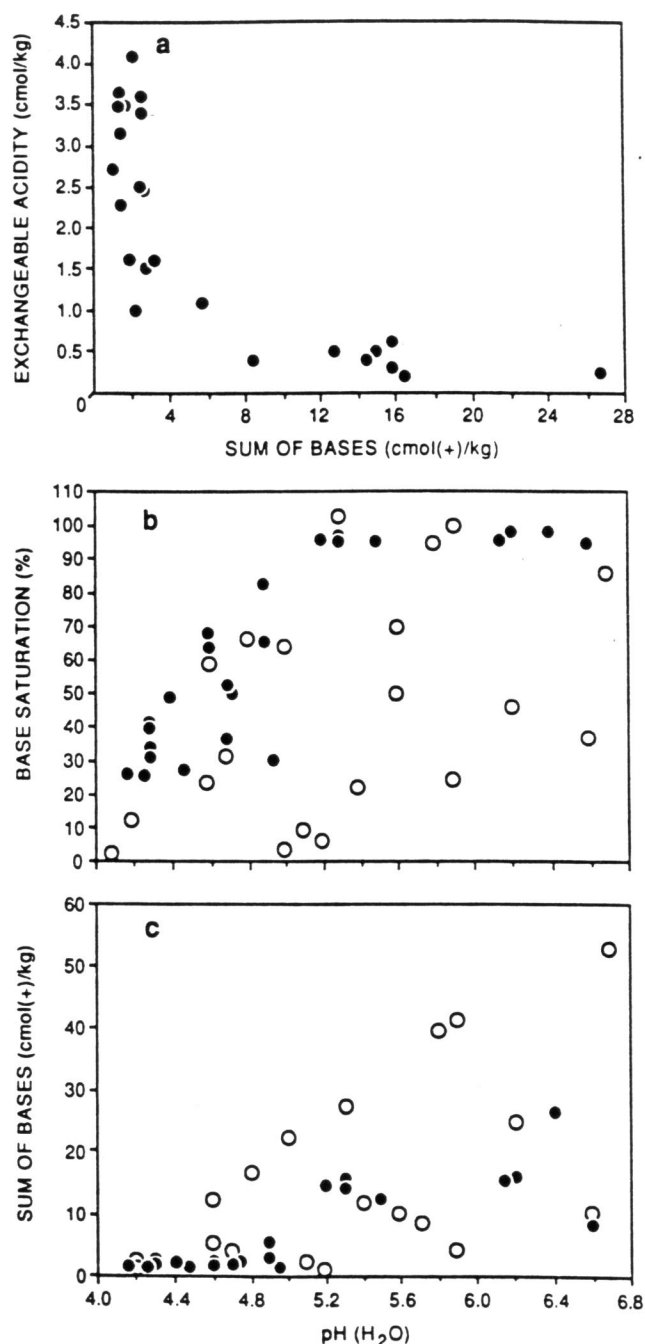


Fig. 4.10. Exchangeable base-metal and acid-metal cations in soils of La Selva (solid circles; data from table 4.1) and other tropical sites (open circles; data from table 4.2): (1) exchangeable acidity (acid cations) compared to sum of base cations; (2) base saturation compared to soil pH in water; (3) sum of base cations compared to soil pH in water.

vegetation-free even for a few months, pH dropped nearly one unit to below the point of zero charge (PZC) (Sollins et al. 1988; Robertson 1989). Laboratory experiments confirmed that the pH drop was the result of increased nitrification, triggered, in turn, because uptake had stopped while mineralization had increased (G. P. Robertson and P. Sollins unpublished data). These large pH drops are important because they mean that (1) base cation levels (K, Mg, Ca), already low, could

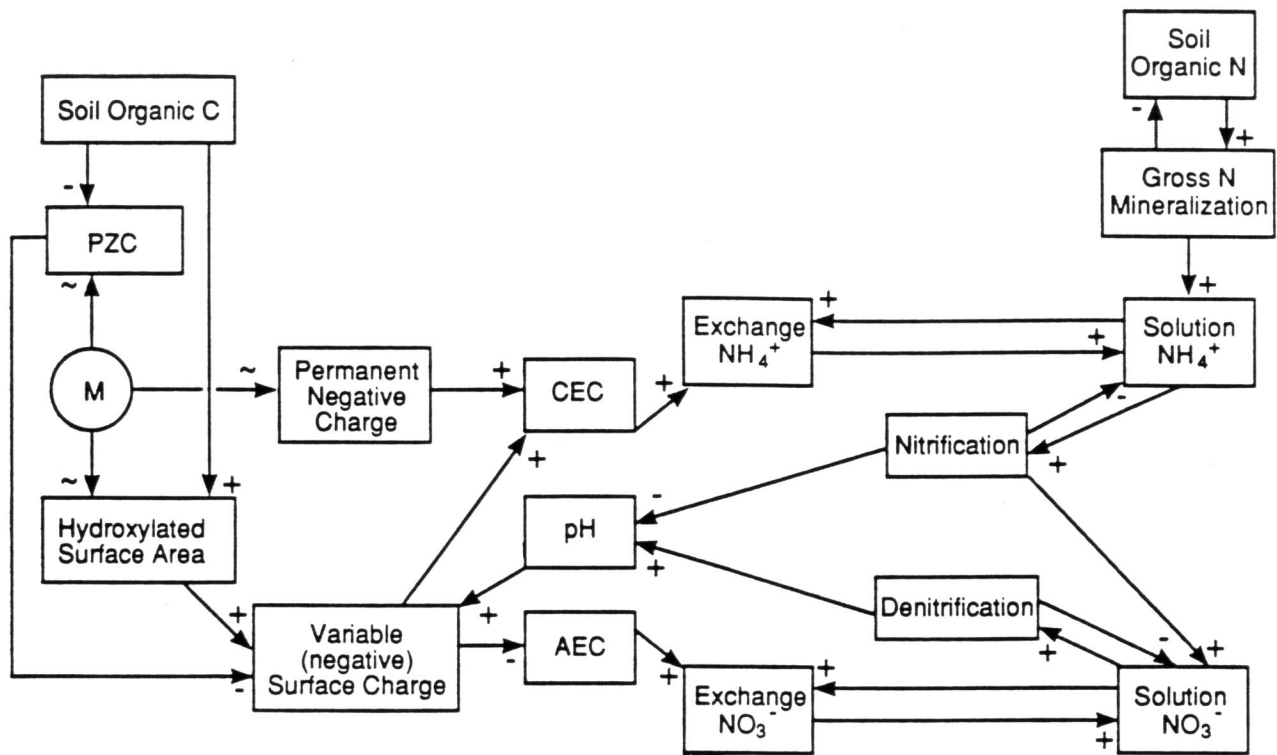


Fig. 4.11. Interactions among charge characteristics, pH, and microbial nitrogen transformations in variable-charge soils (from Sollins et al. 1988). A "+" indicates that the interaction increases the rate or value; a "-" indicates the opposite effect; a "~" indicates that effects are variable. PZC is point of zero charge.

drop even farther as the remaining cations are displaced from exchange sites; (2) CEC decreases, which reduces the ability of the soil to retain cations added in fertilizer or mulch; (3) AEC increases and may even exceed CEC, in which case ammonium will be more mobile than nitrate, the reverse of the situation in the soils from which most of our knowledge of nitrogen dynamics derives; and (4) problems of aluminum toxicity are exacerbated.

Soil pH may also significantly affect soil physical structure. As pH changes, the charge on clay surfaces changes, as does the tendency for the particles to repel each other (Uehara and Gillman 1981; Sollins 1989). From a practical standpoint, this suggests that tropical ecosystems may need to be managed to avoid large and rapid changes in soil pH with attendant effects on nutrient retention and mobility.

Anion Exchange and Adsorption

Anion and ligand exchange are also important processes in variable-charge soils. Anion exchange capacity increases as soil pH approaches the PZC. Because the pH approaches the PZC with increasing depth in the soil, nitrate tends to accumulate in the subsoil (Matson et al. 1987; Sollins et al. 1988). Nitrate accumulation is to be expected in La Selva subsoils, but only low levels of nitrate have been found to date (P. Sollins and G. P. Robertson, unpublished data).

Sulfate adsorption tends to increase with decreasing pH and with increasing levels of iron oxides and allophane (e.g., Uehara and Gillman 1981). Phosphate-extractable S averaged 1.1 cmol (-)/kg at 0- to 15-cm depth and 2.8 cmol (-)/kg at 15- to 30-cm depth (D. W. Johnson et al. 1979); soils used in

this study were taken from just north of OTS plot 1 and belong to the Sainal consociation (D. W. Johnson pers. comm. 1990).

Phosphorus adsorption is common in variable-charge soils and tends to be only weakly pH-dependent below pH 5.5 (Sánchez 1976; Sollins et al. 1988). Although no work has been done on mechanisms controlling phosphorus availability at La Selva, inferences are possible on the basis of the classification of La Selva's soils. Allophane, an extremely strongly phosphorus-sorbing mineral because of its large surface area (Uehara and Gillman 1981), is apparently still present in the less-weathered soils (lower-terrace and some middle-terrace soils); thus, high levels of phosphorus sorption are to be expected. Although allophane is apparently absent from the older soils, goethite appears to be abundant and also sorbs phosphorus strongly (see Sollins et al. 1988).

Vitousek and Denslow (1987) measured extractable phosphorus (acid ammonium fluoride) in surface soil sampled along trails throughout the old La Selva property and Sarapiquí Annex. They found that levels were highest in the lower-terrace soils, intermediate in the upper-terrace soils, and quite low in all the residual soils. Levels were always slightly higher in what are now called the Jaguar than in the Matabuey soils. The more extensive set of surface soil samples collected by Sancho and Mata in 1987 confirmed earlier findings about the three major groups of consociations at La Selva (fig. 4.12) but showed almost no difference between the Jaguar and Matabuey units (see table 4.1); results of phosphorus extraction by a second method (sodium bicarbonate at pH 8.5) showed much less clear patterns even between the lower- and upper-terrace consociations (see fig. 4.12). Bioassays (e.g., Denslow

et al. 1987) suggest that phosphorus availability does, indeed, limit plant growth in many of La Selva's soils (see chap. 5).

Carbon and Nitrogen Levels

La Selva soils vary widely in carbon content. Carbon stores to 1-m depth range from 2 to 25 kg/m² (see table 4.1). By comparison, a set of forested soils in Puerto Rico spanning a wide range of life zones, forest types, soil groups, and topography ranged only from 6.5 to 10.0 kg C/m² (Weaver et al. 1987). At La Selva, all the most carbon-poor soils are sandy riverbank soils, and all the older soils tend to be carbon rich. The correlation between carbon content and soil age is not consistent, however; several of the young alluvial soils (e.g., the Andic Humitropepts of the Holdridge and Experimental units) are among the richest in carbon (>10 kg/m² to 1-m depth). Such high carbon levels likely result from the presence of allophane, which tends to bind or occlude the OM and, thereby, inhibit its decomposition (see Sollins et al. 1988). In the more highly weathered soils at La Selva, the high levels of iron and aluminum oxides and hydroxides (e.g., goethite, gibbsite) are probably responsible, at least in part, for the large amounts of organic matter. In the swamp and valley-bottom soils, organic matter may accumulate because anaerobic conditions hinder decomposition.

Studies suggest that the light fraction of the soil organic matter, mainly partially decomposed plant debris, accounts for only a small portion of the total soil carbon at La Selva. In samples (0–15-cm depth) from an Helechal soil, the light fraction accounted for only 2% of total soil carbon compared to 5%–50% for five temperate-zone soils spanning a wide range of physical structure and mineralogy (Strickland and Sollins 1987). The most likely explanation is that the light-fraction material decomposes more rapidly in tropical than temperate soils. Root turnover studies at La Selva (R. L. Sanford unpublished data) support this hypothesis in that they show very low levels of dead roots despite high rates of root death.

Along with the organic matter, nitrogen has also accumulated in large amounts, and phosphorus and cations rather than

nitrogen tend to limit plant growth (see chap. 5). Why nitrogen has accumulated in such large amounts is not known. Nitrogen fixation by leguminous trees has often been suggested, but results to date are not definitive. With the large range in mineralogy and physical structure in La Selva's soils, the site offers an exceptional opportunity to study mechanisms of OM adsorption on mineral surfaces and the effects of such adsorption on soil organic matter (SOM) turnover and nitrogen mineralization.

RECOMMENDATIONS

Scientists studying tropical ecosystems would benefit greatly from closer collaboration with soil scientists and geologists both when designing studies and when interpreting results. Plant community ecologists, in particular, could use soil and landform classification to much greater advantage, especially when comparing their results with those of others. Several early studies of tropical plant communities (e.g., Ashton 1964) took full advantage of what was known of soils and geology of the region studied, but much recent work has not maintained this momentum. Unless differences among soils are recognized and understood, finding patterns in plant community parameters will be a slow process at best. In general, the lack of soils data for major sites of ecosystem research in the tropics (e.g., Los Tuxtlas, Mexico, and Barro Colorado Island, Panama) continues to make meaningful comparisons impossible.

Even at La Selva, ecosystem and plant community scientists could benefit from a better understanding of the differences in soil types within and among study sites. Probably the biggest single obstacle to progress at La Selva is the lack of topographic information and the inadequacy of the current geographic grid system. The lack of topographic information prevents accurate delineation of terrace boundaries and correlation of soil types between the Río Sarapiquí and Río Puerto Viejo terrace systems. Because grid points are widely spaced and inaccurately located, the sites of most previous studies cannot be pinpointed or assigned unequivocally to a soil mapping unit (see also comments by Vitousek and Denslow 1987). Work currently underway will greatly expand the present 200-m grid and will provide accurate elevations. The grid system will then form the basis for a geographic information system, and as the soil mapping units are redefined, sampling locations can be reassigned readily among soil types.

Methods of soil analysis can affect results markedly, especially in variable-charge soils where measurements at nonambient levels of pH or soil solution composition can grossly distort important soil parameters such as CEC (Uehara and Gillman 1981; Sollins et al. 1988). Those in the Tropical Soil Biology and Fertility Program have attempted to standardize many methods of soils analysis (Anderson and Ingram 1989). Deviation from such standard methods is often warranted but must be noted. Unless methods and locations are documented, results of soils analyses cannot be interpreted or generalized.

La Selva has seen almost no work on animals and plants as factors in soil formation. Soil pH does tend to be lower, for example, around *Pentaclethra* trees, presumably because the trees fix nitrogen, which is then nitrified (P. Sollins unpublished data). Leaf-cutter ants clearly affect soil properties at

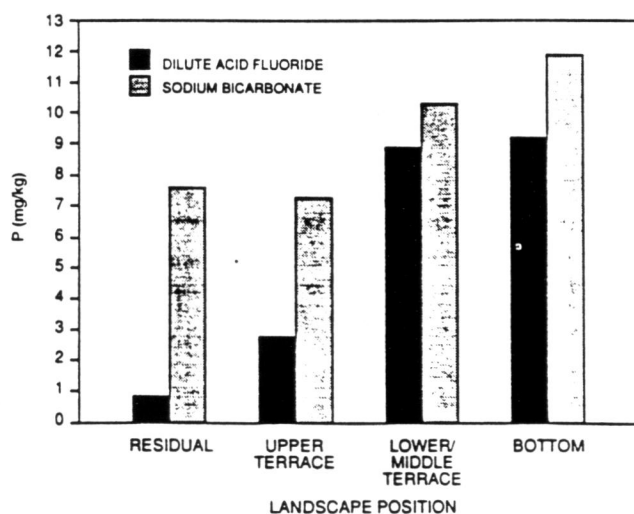


Fig. 4.12. Extractable phosphorus by two methods (acid ammonium fluoride and sodium bicarbonate) for the major groups of soil consociations at La Selva.

La Selva, yet the effects of these animals, and the factors controlling their abundance and activity, remain unstudied. Areas where mammals and reptiles have burrowed or dug for food are also common. With a combination of pasture, second growth, and intact forest on a wide variety of soil types, La Selva provides an ideal setting for such studies.

Researchers have yet to take full advantage of the variability in chemical and physical properties of La Selva's soils. Early work focused on the soils nearest the station: Holdridge, Experimental, and Arboleda. As access to the property improved, emphasis shifted toward the residual soils, but the majority of the lower- and middle-terrace soils have remained little studied, in part because they no longer contain primary forest. As interest in soil chemistry, physics, and microbiology has increased at La Selva, more advantage has been taken of the striking contrasts among the alluvial soils (e.g., the PLOTS project of Robertson and Sollins). In addition, three projects have begun studies on the more highly weathered (presumably older) soils in the hills behind Puerto Viejo (W. A. Reiners and M. Keller, G. Gillman and P. Sollins, R. Butterfield and E. González). The Sarapiquí region, in gen-

eral, provides exceptional opportunities to study effects of parent material, soil age, and colluvial and fluvial processes on soil genesis in a region where climate and mineralogy of the parent material hold nearly constant across a broad area.

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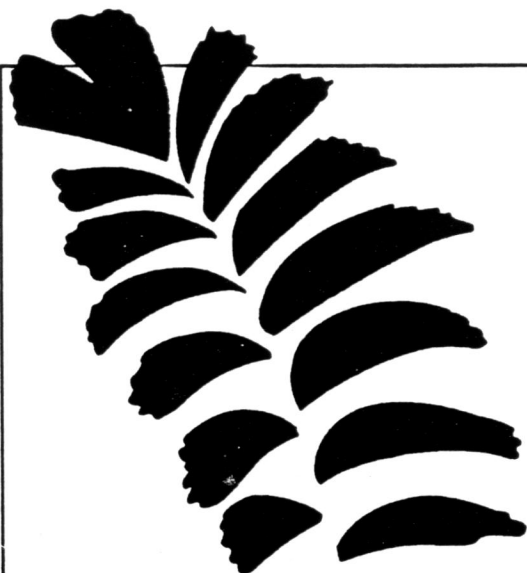
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