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TROPICAL SOIL FERTILITY CHANGES UNDER MONOCULTURES AND SUCCESSIONAL COMMUNITIES OF DIFFERENT STRUCTURE¹

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Abstract. For 5 yr we monitored the fertility of a volcanic-ash derived Inceptisol at a site in the humid tropics of Costa Rica. After forest felling and burning, we established four treatments in a randomized block design with six blocks: a sequence of monocultures (two crops of maize [*Zea mays*] followed by cassava [*Manihot esculenta*], then the tree species *Cordia alliodora*), successional vegetation, a mimic of successional vegetation that was physiognomically similar to the model but shared no species with it, and a species-enriched version of successional vegetation. In addition, one plot was maintained free of vegetation.

Species-rich successional vegetation was effective at maintaining soil fertility, although we observed general trends of soil-nutrient decline beneath all treatments, presumably because of plant uptake. It proved possible to imitate the fertility-maintaining characteristics of successional vegetation by creating an equally species-rich community of different floristic composition, but the maintenance of fertility was not enhanced by further species enrichment.

Successive peaks of nitrate-nitrogen in soil solution, extractable phosphorus, and extractable potassium occurred during the 1st yr, perhaps driven by an early increment of organic matter from postburn debris and roots. Organic matter, total nitrogen, and extractable sulfur were remarkably stable during the 5-yr period.

Depletions of cations, decreases in effective cation exchange capacity (CEC_e), and increases in acid saturation were related to treatment in the following order: bare soil > monocultures > the three diverse, successional communities. In the bare-soil plot, fertility decreased dramatically: there was a net loss of exchangeable cations and inorganic nitrogen, the phosphorus-fixation capacity increased, and acid saturation reached a potentially toxic 86%.

At the start of the study, three of the blocks had soil with lower pH, lower CEC_e, and higher acid saturation. During the study this less fertile soil lost proportionally more cations and increased more in acid saturation and phosphorus-fixation capacity. The less fertile soil under monocultures proved exceptionally vulnerable to loss of fertility; after 5 yr under monocultures, for example, acid saturation reached 38% in the more fertile soil and 75% in the less fertile soil. In the species-rich communities, however, changes in soil fertility were far less marked.

Key words: acid saturation; cations; Costa Rica; fertility; Inceptisol; monoculture; nitrogen; organic matter; phosphorus; succession; sulfur; tropics.

INTRODUCTION

This study was part of an attempt to use ecological theory to design sustainable, low-input agricultural ecosystems for the humid tropics. It was motivated by two observations. First, successional vegetation recolonizing newly deforested tropical soils is usually vigorous and productive; it does not appear to suffer from critical shortages of nutrients except on very poor sites. Second, and in contrast, it is very difficult to sustain

monocultures of annual crops on most tropical soils unless they are heavily subsidized with fertilizers and pesticides; this is true even on the fertile volcanic soils of Central America, where annual cropping requires large inputs of N, P, and S (von Platen et al. 1982, Palmieri 1985). These observations led to the idea of attempting to design agroecosystems modelled on successional vegetation, a concept reviewed by Ewel (1986).

To understand the changes in nutrient availability that occur during the early phases of tropical succession, and to evaluate the potential for using successional communities as models for agroecosystem design, we addressed four questions. (1) What are the magnitudes and directions of soil-nutrient changes during the first 5 yr after forest felling and burning under vegetation of different structure? (2) Do soils that sup-

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port plant communities of similar species richness and physiognomy, but completely different floristic composition, exhibit similar patterns of change in nutrient availability during succession? (3) Will the soil beneath a community that is more species rich than naturally occurring successional vegetation exhibit changes in nutrient availability that are different from those observed in successional vegetation? (4) Will monocultures consisting of the same life form of plants that dominate species-rich successional vegetation differ from successional vegetation with respect to soil-nutrient availability?

The nutrient elements we considered were N, S, P, K, Ca, and Mg. Phosphorus was of particular concern because soils derived from volcanic ash, including those at our study site, generally have high P adsorption capacity (Fox and Searle 1978, Sanchez and Uehara 1980, Tate and Theng 1980, Uehara and Gillman 1981, Zunino et al. 1982). A second important attribute of volcanic soils is that they are dominated by pH-dependent variable-charge minerals; the pH at which the net charge is zero depends on the relative amounts of organic matter and oxides of Fe, Al, and Si in the soil and usually lies between 3.5 and 5.0 (Uehara and Gillman 1981, Sposito 1984). Any land-use practice that affects pH or organic matter content of a variable-charge soil, therefore, is also likely to have a substantial effect on the soil's nutrient-retention properties (Sollins et al. 1988).

STUDY AREA AND METHODS

The study was conducted near Turrialba, Costa Rica, in the Florencia Norte Forest owned by the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). The site is located at 9°53'N, 83°40'W and lies 650 m above sea level. Mean annual rainfall is \approx 2700 mm, and the dry season extends from January through March. The soil is a Typic Dystrandept of the Colorado series (Alvarado et al. 1981). The vegetation at the start of our study consisted of an 8- to 9-yr-old secondary forest plus some remnant patches of 70-yr-old forest dominated by *Goethalsia meiantha* (Donn. Sm.) Burret. Variations in land-use history (e.g., forest that may have once been a coffee plantation, possibly some pasture, and both of these intermixed with former research plots of Harcombe [1977] and CATIE foresters), even on our tiny study area (2.5 ha), likely induced changes in soil fertility that proved important. Specifically, 3 of our 6 blocks fell on a relatively uniform less fertile soil, and 3 fell on an equally uniform more fertile soil, as described in *Results*.

The vegetation on six 33 \times 33 m blocks was felled during the 1st wk in January 1979. Border strips of vegetation, \geq 5 m wide, were left uncut around each plot. Large trunks were removed, and the remaining slash was burned on 22 March 1979. Ewel et al. (1981) described the impacts of site preparation on nutrient balances.

Following the burn, we established four 16 \times 16 m experimental plant communities in each of the six blocks. In addition, one 14 \times 14 m plot was subjected to the same slash and burn treatment as the six larger blocks, but was kept free of vegetation by hand weeding throughout the 5-yr study.

One of the four experimental communities consisted of successional vegetation that colonized by itself, both from seeds and sprouts. A second community, called enriched successional vegetation, also developed by natural colonization, but in addition, at least 10 000 seeds comprised of at least 20 species not native to the site were added monthly to each plot throughout the 5-yr study period. Seeds to be introduced were gathered opportunistically and included exotics as well as natives: the only criterion for selection was that they represented species that could not have gotten to the site without our assistance.

A third community, called imitation of successional vegetation, was designed to mimic the species richness and physiognomy of naturally occurring successional vegetation, but not the floristic composition. We removed naturally occurring colonists and substituted morphologically similar species for them, vine for vine, herb for herb, shrub for shrub, tree for tree, and epiphyte for epiphyte. The introductions included both cultivars and wild species, but did not include any species native to the site.

A fourth community consisted of a temporal sequence of monocultures. For the first 8 mo the successional vegetation was dominated by herbaceous plants, so the first two monocultures (from late March through mid-July and from late-July through November 1979) were maize, *Zea mays* L. From late-November 1979 through mid-September 1980, when the successional vegetation was dominated by low-stature woody vegetation, the monoculture was occupied by cassava, *Manihot esculenta* Crantz, a euphorbiaceous shrub that yields an edible tuber. By the time of the cassava harvest, trees had begun to appear prominently in the successional vegetation, so we planted a monoculture of 1-yr-old seedlings of a native, fast-growing tree, *Cordia alliodora* (Ruiz & Pav.) Oken (Boraginaceae). These trees occupied the monoculture plots until the end of the study in April 1984.

Soil sampling and analysis

From April 1979 through October 1980, when nutrient changes were most rapid, soil samples were taken approximately every 3 mo. From March 1981 until the end of the study in April 1984, soil was sampled twice yearly, in March/April and in September/October.

Soil core locations were determined by randomly selecting a distance along the plot boundary or along an L-shaped access trail in each plot and sampling \approx 1 m off the path. One sample, a composite of soil from eight cores, was taken from each of the six plots per

treatment. During the first 2 yr, soils were sampled at 0–5, 5–25, and 25–45 cm depth intervals after removing the litter. For the last 3 yr of the study, the 45–85 cm depth interval was also included. The first samples taken after the burn (April 1979) extended to a depth of 110 cm.

Soil samples were oven dried at 55°C to retard denitrification, then ground to pass through a 2-mm mesh sieve. Soil pH was determined electrometrically using a soil:water volume ratio of 1:2.5. Soil organic matter and total N, Ca, Mg, K, S, and P were determined on a subsample that was finely ground and passed through a 0.25-mm mesh sieve. Organic matter was determined by the Walkley-Black wet digestion method using a correction factor of 1.33 for unrecovered organic C (Bornemisza et al. 1979) and a ratio of organic matter to organic C of 1.72. Total N was determined by the semimicro Kjeldahl technique (Bremner 1965).

Nitrate-N was measured during the first 18 mo of the study using a specific-ion electrode. At the end of the study, net N-mineralization rates (30-d laboratory incubations) were estimated using methods described in Matson et al. (1987), including extraction of nitrate-N and ammonium-N with 2 mol/L KCl.

Sulfur was extracted with a 500 mg/L $\text{Ca}_3(\text{PO}_4)_2$ solution and determined turbidimetrically (Fox et al. 1964). Exchangeable K, Ca, and Mg were extracted using Mehlich's double-acid method (Sabbe et al. 1974) followed by atomic absorption analysis. This extraction was also used for extractable P, which was determined colorimetrically (Olsen and Dean 1965).

During 1981, 1982, and 1983, P and K were extracted using the modified Olsen method, and Ca and Mg were extracted with an unbuffered 1 mol/L KCl solution (Hunter 1974). To make these data comparable to those for 1979, 1980, and 1984, we extracted 100 samples by both methods and obtained conversion factors using linear regressions. The coefficients of determination for all four elements were >0.8 . We then converted the 1981–1983 data to their double-acid-extraction equivalents.

Exchangeable acid ($\text{H}^+ + \text{Al}^{3+}$) was extracted with 1 mol/L KCl and determined by titration (Coleman et al. 1959). Effective cation exchange capacity (CEC_e) was calculated as the sum of exchangeable acidity, Ca, Mg, and K. Acid saturation is the percentage of CEC_e accounted for by exchangeable acid.

Anticipating that our volcanic-ash-derived soil would have high P-fixation capacity, we constructed sorption isotherms (Fox and Kamprath 1970) for soil sampled at depths of 0–5 and 5–25 cm. Phosphorus in the equilibrium solution was determined colorimetrically (Murphy and Riley 1962). The P-fixation capacity was evaluated for two types of vegetated plots (successional vegetation and monoculture) and for the bare plot. Isotherms were constructed for one set of soil samples taken early in the study (August 1979) and another set taken near the end (October 1983).

Total cations, P, and S were extracted by digestion with nitric-perchloric-hydrochloric acid (3:4:1 ratio). Total Ca, Mg, and K were determined by atomic absorption, P by colorimetry (Olsen and Dean 1965), and S by turbidimetry (Fox et al. 1964).

RESULTS

Our findings are presented in three sections: the first deals with organic matter and elements present primarily in organic forms (N, P, and S), the second with cations, and the third with acidity. Summary tables (1, 5, and 6) compare treatments and soil depths 5 mo after the start of the study and at the end of the study. Representative time courses (Figs. 1, 2, 4, 5, 6) contain data based on weighted means of values obtained from 0 to 5 cm and 5 to 25 cm. The uppermost 25 cm of soil was sampled as a single horizon at the start of the study, so the graphs (unlike the tables) begin immediately after the slash was burned in 1979. The surface 25 cm is also the zone where most roots are located (Berish and Ewel 1988) and where marked changes in nutrient availability occurred. Data in Mazzarino et al. (1988) overlap, in part, with some data in this paper, but contain errors. They should be supplanted by data in Tables 1, 5, and 6 and Figs. 1 and 3.

Most data are summarized as means of measurements from all six blocks. Although the study site comprised only 2.5 ha, we found that 3 of the 6 blocks differed significantly (ANOVA, $\alpha = .05$) from the others in acidity and extractable cations; therefore, data for the more fertile group and the less fertile group are presented individually. The bare plot was on the less fertile soil. In some cases we compare values to those in the surrounding forest, sampled only at the beginning of study.

Statistical analyses of temporal trends are summarized for all variables that yielded linear time courses in Table 2. Statistical analyses of differences that were brought about by 5 yr of site occupancy by the four different kinds of vegetation are summarized in Table 7.

Organic matter, nitrogen, phosphorus, and sulfur

Organic matter.—Like many other volcanic soils, those at our site contained large amounts of organic matter (Table 1). The organic matter content of the soil decreased during the 5-yr study in all communities studied (Table 2), but the decline was more dramatic in the bare plot than in vegetated plots. However, because the organic matter in volcanic soils forms complexes with allophane and is refractory (Wright 1964), the soil in the bare plot contained an average of $>5\%$ organic matter throughout the profile (0–85 cm), even after 5 yr without vegetation.

Organic matter changes in the soil did not differ among the diverse communities (successional vegetation, enriched successional vegetation, and imitation

TABLE 1. Concentrations of organic matter and associated nutrients in the soil under five treatments near the beginning and at the end of the 5-yr study. All values are means from six replications except for the unreplicated bare plot. Totals are means from four sampling dates, August 1979 through July 1980. ND = no data.

Vegetation	Soil depth (cm)	Organic matter (%)		Nitrogen (%)		C:N		Phosphorus (mg/kg)			Sulfur (mg/kg)		
		5 mo	61 mo	5 mo	61 mo	5 mo	61 mo	Extractable		Total	Extractable		Total
								5 mo	61 mo		5 mo	61 mo	
Succession	0-5	16.5	13.6	.75	.73	13.0	10.7	7.9	3.1	992	39.3	38.0	1281
	5-25	9.4	7.0	.39	.43	14.2	9.3	1.3	1.7	838	37.2	35.0	1130
	25-45	8.3	6.1	.30	.31	16.0	11.6	1.2	1.9	721	34.9	34.6	1065
	45-85	ND	5.1	ND	.25	ND	11.6	ND	1.6	ND	ND	43.1	ND
Enriched succession	0-5	14.4	12.3	.69	.75	12.1	9.6	5.8	5.8	1024	36.5	36.9	1267
	5-25	8.9	6.6	.39	.41	13.1	9.3	1.5	1.4	853	36.6	37.3	1248
	25-45	8.1	5.3	.32	.31	15.0	9.9	1.2	2.0	769	37.8	38.7	1239
	45-85	ND	4.3	ND	.25	ND	10.2	ND	1.6	ND	ND	38.7	ND
Imitation of succession	0-5	16.3	12.7	.76	.74	12.4	9.9	8.0	4.0	992	39.8	29.4	1354
	5-25	9.2	7.2	.39	.41	13.9	10.2	1.2	1.7	821	37.2	31.0	1253
	25-45	8.5	5.6	.33	.31	14.8	10.8	1.1	1.7	754	37.0	38.3	1123
	45-85	ND	4.7	ND	.25	ND	10.9	ND	1.6	ND	ND	46.1	ND
Monoculture	0-5	16.8	11.9	.78	.62	12.5	11.6	7.7	2.9	880	31.6	27.9	1303
	5-25	9.1	6.8	.41	.41	12.9	9.5	1.3	1.6	761	34.6	36.9	1159
	25-45	8.1	5.8	.33	.30	14.4	11.2	1.1	1.9	734	32.8	39.6	1188
	45-85	ND	4.5	ND	.26	ND	10.8	ND	2.0	ND	ND	35.7	ND
Bare	0-5	16.5	9.0	.75	.54	12.7	10.0	2.8	4.4	912	36.8	28.7	1354
	5-25	11.8	7.5	.54	.38	12.7	11.4	1.3	1.8	744	16.2	37.9	1132
	25-45	11.4	6.7	.39	.31	16.9	12.5	1.3	1.7	626	22.8	36.6	1086
	45-85	ND	4.5	ND	.24	ND	10.9	ND	2.4	ND	ND	24.6	ND

of successional vegetation), so mean values for these three treatments were combined before they were plotted (Fig. 1). During the first 5-12 mo, organic matter increased in the upper 25 cm of soil in all plots and was greatest in the bare plot. Organic matter declined during the next 2 yr, but was high and constant for the final 2 yr of the study, even in the bare plot.

Nitrogen.—Most soil N at our site is in organic forms, so it tended to be high, like organic matter, and remarkably stable throughout the 5-yr study (Tables 1 and 2). Soil N declined significantly only in the surface 5 cm of the bare plot and the monoculture. By the end

of the 5-yr study the N content of the soil in all vegetated treatments was even higher (mean = 0.48%) than that of the original forest (0.38%).

Nitrate-N was high early in the study, then diminished in vegetated plots before again increasing during the 2nd yr (Table 3). In the bare plot, values were extremely high until the 2nd yr, when the effects of sustained leaching and lack of organic nitrogen replenishment became apparent. In general, high values in the bare plot and monoculture were associated with the dry season; in the diverse communities nitrate uptake presumably continued in the dry season, so values

TABLE 2. Significance of temporal changes in soil characteristics, 0-25 cm. - indicates a significant negative slope (probability < .05 of a larger *t* for the test of a null hypothesis of slope = 0), + indicates a significant positive slope, and 0 indicates no significant change with time. ND = no data.

Variable*	Fertility group	Treatment				
		Succession	Enriched	Imitation	Monoculture	Bare
Organic matter	combined	-	-	-	-	-
Nitrogen	combined	0	0	0	0	0
Calcium	higher	0	0	0	-	ND
	lower	-	0	0	-	-
Magnesium	higher	0	0	-	-	ND
	lower	-	0	-	-	-
CEC _e †	higher	0	0	0	-	ND
	lower	-	-	-	-	-
pH	combined	0	-	-	-	0
Acid saturation	higher	0	0	0	+	ND
	lower	0	0	0	+	+

* Phosphorus and potassium are not included because their changes with time were decidedly nonlinear; sulfur is excluded because there are no data for the earliest sampling date.

† Effective cation exchange capacity.

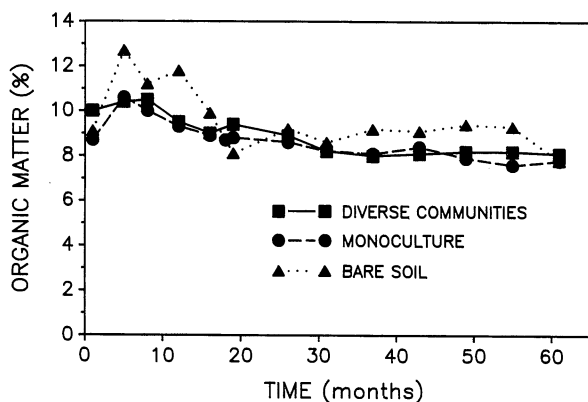


FIG. 1. Changes in organic matter in the upper 25 cm of soil. The diverse vegetation is a mean of successional vegetation, an imitation of successional vegetation, and enriched successional vegetation. Values are means of six replications per treatment except for the unreplicated bare plot.

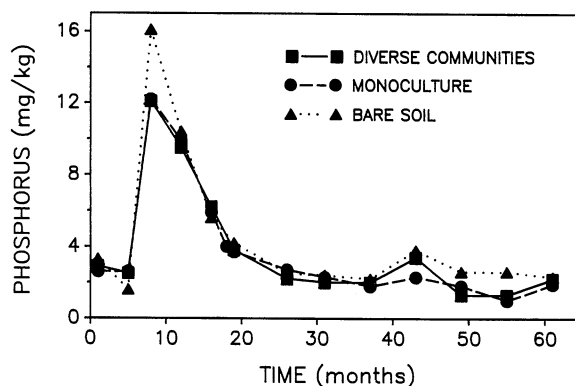


FIG. 2. Changes in extractable phosphorus in the upper 25 cm of soil. The diverse vegetation is a mean of successional vegetation, an imitation of successional vegetation, and enriched successional vegetation. Values are means of six replications per treatment except for the unreplicated bare plot.

remained low throughout the year. Routine measurements of soil nitrate were terminated after 18 mo, but after 5 yr, values in all treatments were very low: 4–7 mg/kg in the upper 15 cm, compared to a weighted mean of 40 mg/kg at the start of the study.

Ammonium-N, measured only at 5 yr, was significantly higher in the successional and enriched successional vegetations (10.6 mg/kg in the upper 15 cm) than in the imitation of succession and the *Cordia alliodora* monoculture (mean = 7.5 mg/kg); the bare plot had only 5.1 mg/kg. Net N-mineralization rates (30-d laboratory incubations) at this time ranged from 46 to 60 mg/kg (overall mean = 55 mg/kg) in soil from the vegetated plots and did not differ significantly (ANOVA, $\alpha = .05$) among treatments; rates were substantially lower (41 mg/kg) in the bare plot.

Carbon:nitrogen ratio.—Because soil C decreased while N remained relatively constant, there was a general tendency for the C:N ratio to decline in all communities (Table 1). In August 1979, for example, the average ratio of C to N ranged from 12.1 to 16.9, but these ratios dropped over the next 5 yr to a range of 9.3–12.5. In 3 of the 5 treatments, i.e., succession, imitation of succession, and the bare plot, the highest C:N ratios occurred after the first 7–12 mo, in synchrony with the early increase in soil organic matter.

Phosphorus.—Concentrations of extractable P, which accounted for <1% of the total amount of P present (Table 1), were very low in our soils. The differences between the amounts present at the beginning (just after the burn) and end of the study were not significantly different (except in the surface 5 cm of soil), but the changes during the first 2 yr were spectacular (Fig. 2). These changes were evident at all depths, but were most pronounced near the surface. During the first 8 mo, for example, the amount of extractable P in the surface 5 cm increased from ≈ 7 mg/kg to >20 mg/kg in the vegetated plots and to 40 mg/kg in the bare plot;

during the next 16 mo they decreased almost as precipitously as they had increased. At the end of the study, extractable-P concentrations in the surface 25 cm of soil (Fig. 2) were very low (1.5 mg/kg), only slightly higher than those of the soil beneath the forest we had felled and burned to create the plots 5 yr earlier (1.3 mg/kg).

Representative P sorption curves, in which the slope described the relationship between P in solution and the P sorption capacity of the soil, illustrate that the soil at our site had a capacity to adsorb large quantities of P (Fig. 3). The slope was steeper in the less fertile soil than in the more fertile soil. Phosphorus-fixation capacity increased in all treatments during the 5-yr study (Table 4), especially in the uppermost 5 cm. The most pronounced increase occurred in the surface soil of the bare plot. Although the P-fixation capacity of

TABLE 3. Nitrate-nitrogen (mg/kg) during the first 18 mo after forest clearing and burning. Values are means from each of six blocks.

Vegetation	Depth (cm)	Time after burn (mo)				
		5	8	12	16	18
Diverse*	0–5	24 (60)	3	7	11	27
	5–25	22 (39)	3	5	16	21
	25–45	19 (35)	3	4	13	19
Monoculture	0–5	84	9	47	8	67
	5–25	73	11	19	20	38
	25–45	24	3	4	13	19
Bare	0–5	96	93	180	30	33
	5–25	14	127	160	98	100
	25–45	87	86	50	67	65

* Two values are given for diverse vegetation at 5 mo; the first value is the mean of successional and enriched successional vegetation, and the parenthetical value is for the imitation of succession, which differed significantly from the other two on that date only (ANOVA, $\alpha = .05$). All other values for diverse vegetation are means from those three kinds of vegetation.

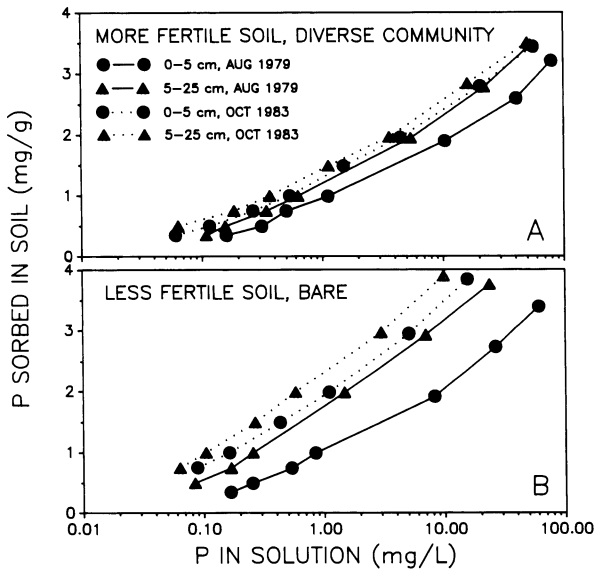


FIG. 3. Phosphorus sorption isotherms for soil from two depths, sampled early in the study and 4 yr later. These examples represent our two extreme conditions. (A) More fertile soil covered by successional vegetation. (B) Less fertile soil kept free of vegetation.

the more fertile soil was higher than that of the less fertile soil, the relative increase in P-fixation capacity during the study was greatest in the surface 5 cm of the less fertile soil.

Sulfur.—Sulfur was distributed more uniformly among soil depths than any other element studied (Table 1). Extractable S accounted for 3–4% of the total amount present, most of which was presumably bound in organic matter. We have no S data from the initial soil samples, but after 5 mo concentrations of extractable S at depths >25 cm were lower in the bare plot than in soils that supported vegetation. Nevertheless, during the next 56 mo extractable S concentrations at depth increased in the bare plot to values comparable to those in the other treatments. These increases in S with depth were accompanied by decreases in S concentrations in the surface soil, suggesting that S in the surface soil moved downward and was not replaced.

Cations and cation exchange

Potassium.—The concentrations of both extractable K and total K in the soil at our site were medium to low in comparison with other tropical soils (Table 5). Extractable K decreased markedly with soil depth, while total K diminished only slightly. Extractable K accounted for $\geq 30\%$ of the total K in the surface soil but only 5–10% deeper in the profile. There was significantly more extractable K in the surface 25 cm of the more fertile soil than in the less fertile soil, but the differences were modest compared to those of other cations.

With few exceptions, concentrations of extractable K were lower at the end of the study than at the beginning (Table 5). The decline was greater and more consistent at a soil depth of 5–25 cm than it was on the surface, where much K was probably held by organic matter, or deeper in the profile, where K was probably retained by clays. This general trend of a decline with time was interrupted by a dramatic increase in March 1980, which was at the height of the dry season, 1 yr after the plots were established (Fig. 4). At the end of the study the uppermost 25 cm of soil on all the plots contained less K than the 130 mg/kg that had been present in the forest at the start of the study, prior to forest felling and burning.

Calcium.—Extractable and total Ca both decreased with soil depth (Table 5). The amounts of extractable Ca differed by as much as 50%, more than any other cation measured, between the two soil-fertility groups. In the surficial 25 cm, extractable Ca accounted for an average of 23 and 11% of the total Ca in the better and poorer soil, respectively. Deeper in the profile, extractable Ca constituted an average of 12% of the total in both soils.

Extractable Ca, which accounted for 60–80% of the base saturation at the start of the study, declined significantly over 5 yr in the monocultures and in the bare plot (Table 2). In the monocultures, the absolute amount of Ca lost from the more fertile soil was greater than the amount lost from the less fertile soil. Nonetheless, the relative amount lost from the less fertile soil was far greater: 71% compared to 43%. The extractable Ca content of the surficial 25 cm of soil in the monoculture on the more fertile soil decreased to values similar to those of the less fertile soil 5 yr earlier.

Magnesium.—Concentrations of extractable Mg were highest in the surface soil and decreased with depth (Table 5). Total Mg, however, was relatively constant below the surface 5 cm. Extractable Mg accounted for 5–10% of the total Mg in the surficial 25 cm and $\approx 5\%$ deeper in the profile.

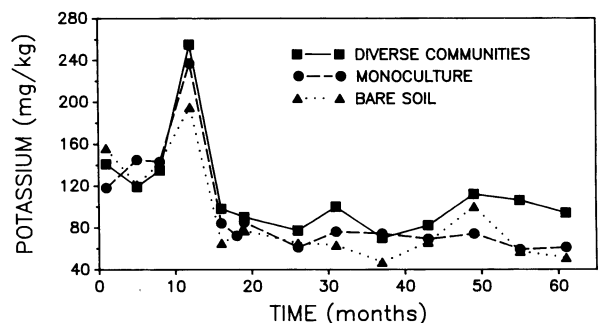


FIG. 4. Changes in extractable potassium in the upper 25 cm of soil. The diverse vegetation is a mean of successional vegetation, an imitation of successional vegetation, and enriched successional vegetation. Values are means of six replications per treatment except for the unreplicated bare plot.

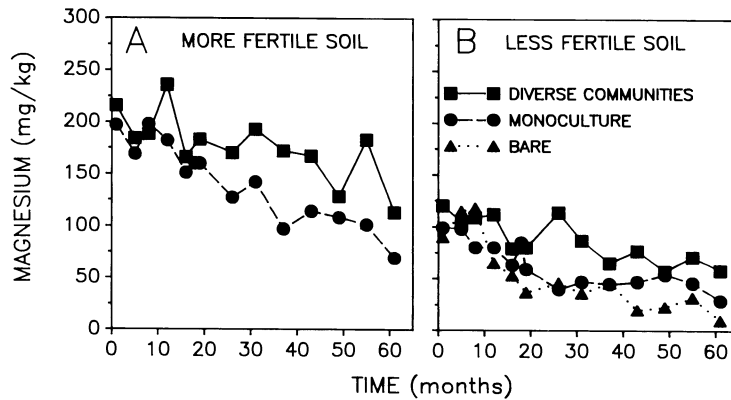


FIG. 5. Changes in extractable magnesium in the upper 25 cm of soil. The diverse vegetation is a mean of successional vegetation, an imitation of successional vegetation, and enriched successional vegetation. Values are means of three replications per treatment except for the unreplicated bare plot. (A) More fertile soil. (B) Less fertile soil. Note that the more fertile soil lines end at values similar to the starting points for the less fertile soils.

Extractable Mg tended to decrease with time in all treatments (Fig. 5), although in some of the diverse communities the declines were not significant (Table 2). The absolute losses were greatest from the more fertile soil. For example, the monocultures lost extractable Mg from the surface 25 cm at average annual rates of 26 and 14 mg/kg from the more and less fertile soils, respectively. The relative losses, however, were greatest from the less fertile soil, which had substantially less Mg to start with.

Cation exchange capacity.—The surface horizon of the more fertile soil at our site had CEC_e values that were medium in comparison with other tropical soils, whereas the CEC_e of the surface horizon of the less fertile soil was low (Table 5). At the start of the study, the pH of the less fertile soil (4.9) was lower than that of the more fertile soil (5.4). Because the CEC_e of variable-charge soils is pH dependent, this probably accounts for the initial differences in CEC_e . Also, at pH < 5.0, Al forms hydroxy-Al complexes that can be deposited on clays and are difficult to displace, resulting in a substantial reduction in CEC_e (Ulrich 1981); this

too may have contributed to the low CEC_e of our less fertile soil.

Absolute values of CEC_e , as well as the variability of those values, decreased with depth on all plots; below 25 cm the CEC_e of both the less fertile soil and the more fertile soil were low. The decrease in variability of CEC_e with depth was probably due to the increased role of clays in cation exchange in deeper soils as opposed to the predominant role of organic matter near the surface.

The CEC_e from 0 to 25 cm decreased on all poorer soil plots with time (Table 2). The decrease was greatest on the bare plot, followed by the monocultures, which declined in CEC_e at about the same rate in both soil-fertility groups.

Acidity

pH.—The soil pH was slightly higher in the surface 5 cm than deeper in the profile (Table 6). The average pH of the surface 25 cm ranged from 3.9 (after 37 mo in the bare plot) to 5.4 (initial condition of the more fertile soil) during the study; the pH of the better soil

TABLE 4. Changes in phosphorus sorption (mg/kg) by the more fertile and less fertile soils (0–25 cm) under successional vegetation, monocultures, and bare soil. Data are based on a standard P solution containing 0.2 mg/L, which is thought to represent the extractable P concentration required by many crops; many tropical crops may have lower P requirements (Sanchez and Uehara 1980).

Soil fertility group	Soil depth (cm)	Vegetation	Time after burn (mo)		Increase (%)
			5	55	
More fertile	0–5	succession	625	765	22
		monoculture	665	875	32
	5–25	succession	1120	1320	18
		monoculture	1100	1300	18
Less fertile	0–5	succession	400	575	44
		monoculture	400	675	69
		bare	415	850	105
	5–25	succession	665	775	16
		monoculture	875	1025	17
		bare	1100	1325	20

TABLE 5. Concentrations of extractable and total cations and effective cation exchange capacity (CEC_e) in the soil under five treatments near the beginning and at the end of the 5-yr study. Values to the left of a solidus are means of three replications from the more fertile soil, and values to the right of a solidus are means of three replications from the less fertile soil, for depths that differed significantly (ANOVA, alpha = .05) between the two soil-fertility groups. The unreplicated bare plot

Vegetation	Soil depth (cm)	Potassium (mg/kg)			Calcium (mg/kg)		
		Extractable		Total	Extractable		Total
		5 mo	61 mo		5 mo	61 mo	
Succession	0-5	135/157	199/130	764	2431/1221	1888/788	5575
	5-25	126/77	75/51	588	742/247	487/173	3644
	25-45	51	62	571	343	298	3618
	45-85	ND	28	ND	ND	271	ND
Enriched succession	0-5	150/139	306/181	778	1756/831	1745/971	6452
	5-25	124/65	99/54	662	547/279	410/181	3549
	25-45	67	55	631	384	273	3255
	45-85	ND	36	ND	ND	213	ND
Imitation of succession	0-5	319/196	203/111	798	2638/786	1741/615	5912
	5-25	158/101	93/54	691	851/605	245/186	3800
	25-45	91	56	641	448	283	3586
	45-85	ND	35	ND	ND	239	ND
Monoculture	0-5	230/197	103/69	748	2159/965	1253/310	5136
	5-25	146/112	51/57	639	609/240	374/101	3186
	25-45	89	32	576	363	202	2938
	45-85	ND	29	ND	ND	187	ND
Bare	0-5	196	54	782	1266	125	4494
	5-25	102	51	643	346	63	3396
	25-45	86	30	591	310	57	3052
	45-85	ND	26	ND	ND	51	ND

was consistently ≈ 0.5 units higher than that of the poorer soil.

The treatments did not differ significantly in their effects on surface-soil acidity (Table 7). For the first 3 yr pH declined in the surface 25 cm in all treatments, reaching its lowest values in April and October 1982,

when the plots were 3-3.5 yr old. Soil pH gradually increased during the final 1.5-2 yr, eventually returning to values only slightly lower than those observed at the start of the study.

Acid saturation.—Acid saturation, like CEC_e, is a useful overall indicator of cation status because it is a

TABLE 6. pH and acid saturation of the soil under five treatments near the beginning and at the end of the 5-yr study. Acid-saturation values to the left of a solidus are means of three replications from the more fertile soil and values to the right of a solidus are means of three replications from the less fertile soil, all of which differed significantly (ANOVA, alpha = .05). The unreplicated bare plot was on the less fertile soil.

Vegetation	Soil depth (cm)	pH		Acid saturation (%)	
		5 mo	61 mo	5 mo	61 mo
Succession	0-5	5.8	5.1	1/7	3/17
	5-25	4.9	4.7	14/57	29/70
	25-45	4.8	4.8	31/63	42/65
	45-85	ND	4.9	ND	27/62
Enriched succession	0-5	5.3	5.1	2/16	3/18
	5-25	4.9	4.6	30/61	32/68
	25-45	4.9	4.7	25/64	36/73
	45-85	ND	4.7	ND	34/71
Imitation of succession	0-5	5.2	5.1	1/17	4/33
	5-25	5.0	4.7	8/59	23/66
	25-45	4.8	4.7	15/60	35/76
	45-85	ND	4.7	ND	31/72
Monoculture	0-5	5.3	4.9	1/15	11/51
	5-25	4.7	4.6	16/63	45/81
	25-45	4.7	4.6	20/68	53/84
	45-85	ND	4.6	ND	43/78
Bare	0-5	5.2	4.5	3	80
	5-25	4.4	4.4	47	87
	25-45	4.5	4.6	51	88
	45-85	ND	4.5	ND	88

was on the less fertile soil. Totals are means from four sampling dates, August 1979 through July 1980.

Magnesium (mg/kg)			Cation exchange capacity (cmol/kg)	
Extractable			5 mo	61 mo
5 mo	61 mo	Total	5 mo	61 mo
310/312	225/168	2207	15.2/9.7	12.1/6.8
159/80	102/31	2051	5.4	4.5
78	56	1925	4.6	4.4
ND	53	ND	ND	3.3
305/207	216/157	2719	11.9/7.4	11.6/8.0
132/69	74/35	1930	5.4	4.2
86	53	1849	4.9	4.1
ND	43	ND	ND	3.3
355/187	205/117	2294	17.1/7.2	11.3/6.4
183/69	88/41	1934	5.8	4.5
104	56	1890	5.1	4.2
ND	50	ND	ND	3.4
309/229	169/66	2125	14.1/8.4	8.7/4.7
135/65	44/20	1878	5.4	4.4
82	33	1790	4.7	4.2
ND	32	ND	ND	3.4
240	18	2071	9.1	4.5
84	8	1935	5.1	4.1
69	8	1990	4.7	3.6
ND	5	ND	ND	3.0

measure of the percentage of the exchange sites that are occupied by Al and H. Acid saturation, more than any other variable measured, differed markedly between the two soil-fertility groups. Furthermore, the

differences in acid saturation between the two soils extended throughout the profile. At the start of the study acid saturation ranged from ≈ 1 to 31% in the better soil and 7 to 68% in the poorer soil; saturation was consistently lower in the surface 5 cm than deeper in the profile (Table 6).

Acid saturation did not increase significantly during the 5-yr study in the three most diverse communities on either soil type (Fig. 6, Table 2). Differences at the end of the study in the soils occupied by the three diverse communities reflected differences that had been present at the start: 15% acid saturation in the more fertile soil and 50% in the less fertile soil.

In the monocultures, acid saturation increased in both soils at average rates of 4–5%/yr (Fig. 6), but the pattern of change differed between the two. In the more fertile soil, acid saturation was almost constant for the first 3.5 yr of the study, then doubled during the last 1.5 yr. The increase was gradual and continuous in the less fertile soil. Because the initial acid saturation of the less fertile soil was so high (53%), by the end of the study it had increased to 75% under monocultures. Nowhere did acid saturation increase more dramatically than in the bare plot, where it increased at an average rate of almost 10%/yr and reached 86% at the end of the study (Fig. 6).

DISCUSSION

Changes in nutrient availability

Organic matter, nitrogen, phosphorus, and sulfur.— The organic matter content of the soil at our site, like

TABLE 7. Treatment differences in soil characteristics at the end of the 5-yr study. Within a column, the soil characteristic at a particular depth did not differ significantly (ANOVA, $\alpha = .05$) among treatments followed by the same letter. A – indicates no significant difference among treatments.

Depth (cm)	Treatment	Soil characteristic*							
		N	S	Ca	Mg	K	CEC _e	pH	Acid saturation
0–5	Succession	a	a	a, b	a	b	b	–	b
	Enriched	a	a	a	a	a	a	–	b
	Imitation	a	b	b	b	b	b	–	a, b
	Monoculture	b	b	c	c	c	c	–	a
5–25	Succession	–	–	a, b	a, b	–	–	–	a, b
	Enriched	–	–	a, b	a, b	–	–	–	a, b
	Imitation	–	–	a	a	–	–	–	b
	Monoculture	–	–	b	b	–	–	–	a
25–45	Succession	–	–	a	–	a	–	a	b
	Enriched	–	–	a, b	–	b	–	a, b	a, b
	Imitation	–	–	a, b	–	b	–	a, b	a, b
	Monoculture	–	–	b	–	b	–	b	a
45–85	Succession	–	–	–	–	a	–	a	–
	Enriched	–	–	–	–	a, b	–	b	–
	Imitation	–	–	–	–	b	–	b	–
	Monoculture	–	–	–	–	b	–	b	–

* Nitrogen values were totals; those for other elements were extractables. Phosphorus and organic matter are not shown because there were no differences among treatments. For N and S, all replications were combined because there were no differences between the more fertile and less fertile soils. For all other variables, only results of data analyses from the poorer soil are included because, except for the following, there were no differences among treatments on the richer soil: Mg at 5–25 cm, S^a, E^{a,b}, I^{a,b}, M^b, where S = succession, E = enriched succession, I = imitation succession, and M = monoculture. At the start of the study there were no significant differences among treatments, with the following exceptions: Mg at 0–5 cm, S^a, E^b, I^b, M^{a,b}; K at 5–25 cm, S^{a,b}, E^b, I^{a,b}, M^a; and pH at 0–5 cm, S^a, E^{a,b}, I^b, M^{a,b}.

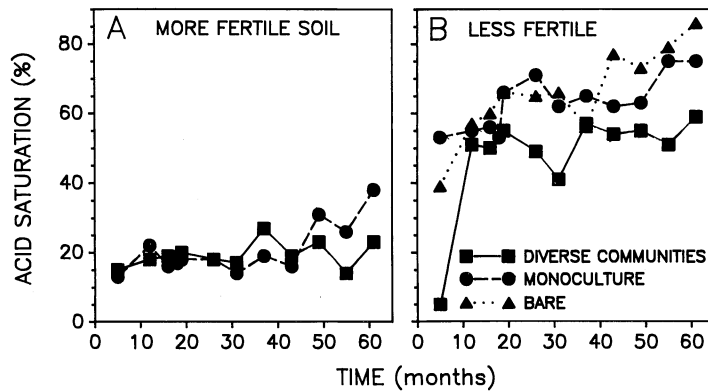


FIG. 6. Changes in acid saturation in the upper 25 cm of soil. The diverse vegetation is a mean of successional vegetation, an imitation of successional vegetation, and enriched successional vegetation. Values are means of three replications per treatment except for the unreplicated bare plot. (A) More fertile soil. (B) Less fertile soil. Note that the more fertile soil lines end at values similar to the starting points for the less fertile soils.

that of volcanic soils throughout the world (Wright 1964), was high. Within a few months following clearing and burning, there was an increase in organic matter of $\approx 1\text{--}2\%$ due to incomplete combustion, root disintegration, and the incorporation of charred fragments of vegetation into the soil. This pulse of organic matter may have provided the energy needed to drive the microbial processes that resulted in successive peaks of nitrate N, extractable P, and K (Fig. 7), as described later in this section. Similar increases, though less pronounced than those we observed, have been reported by Nye and Greenland (1960) and Seubert et al. (1977). Within 2.5 yr organic matter content declined to $\approx 8\%$ in the top 25 cm of soil, which was similar to the amount (7.9%) in the forest that occupied the site prior to our experiments. Likewise, the N content of the soil was nearly constant throughout the study, especially in the plots with diverse vegetation. This contrasts with findings reported for tropical soils with lower contents of stable organic matter (Cunningham 1963, Aweto

1981, Williams-Linera 1983) but is typical of volcanic soils (Suarez de Castro 1957, Sanchez 1976).

What might account for this remarkable stability of soil organic matter and N in a warm, wet climate? Sollins et al. (1984) analyzed the soil organic matter at our site and found that, like other volcanoclastic soils of the lowland humid tropics, the light fraction (i.e., macroorganic matter) comprised only 1.6% of the soil mass ($\approx 20\%$ of the total organic matter) and had a C:N ratio of 19 (compared to values of 10–12 for total organic matter). In many soils, it is the heavy fraction of organic matter (i.e., humus) that participates most actively in mineralization (Bernhard-Reversat 1981), but the heavy fraction of volcanic soils is extremely stable (Sollins et al. 1984). This is because allophane particles (which have high specific surface area and, therefore, large capacity to sorb organic matter) coalesce around organic matter, protecting it from microbial attack and forming extremely stable aggregates (Sollins et al. 1988). At our site the preponderance of a less reactive heavy

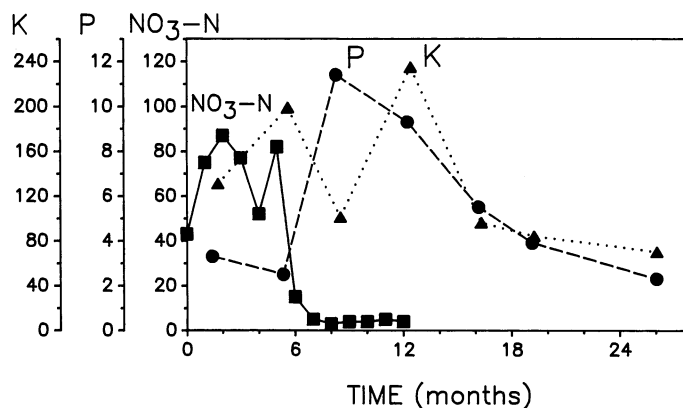


FIG. 7. Sequential peaks in nitrate-nitrogen, extractable phosphorus, and extractable potassium in the upper 25 cm of soil beneath successional vegetation ($n = 6$) early in the 5-yr study. Values are mg/kg.

fraction may have led to the stability of organic matter and N.

The amount of organic N in the soil is immensely higher (2–3 orders of magnitude) than that of N in forms available to plants; it is the rate of mineralization of the organic N that determines N availability. A parallel study at our site (Matson et al. 1987) revealed that N mineralization increased sharply during the first 5 mo after clearing, then declined to rates similar to those of the surrounding forest. By the time the plots were 5 yr old, the N-mineralization rate of the bare plot was $\approx 50\%$ lower than that on the vegetated plots, presumably because of the nonreplenishment of fresh organic matter on the plot with no vegetation. The lack of significant differences in laboratory rates of N mineralization in soil from the vegetated plots indicates that the quality of organic matter (an important determinant of N-mineralization rates) was similar in all four treatments, despite great differences in species composition.

The amount of extractable P in the soil at our site was extremely low, even though the total amount of P present was substantial. A shortage of P also can slow N mineralization and organic matter breakdown (Purchase 1974, Sollins et al. 1988), and this too may have contributed to the relative stability of organic matter and N. Phosphorus fixation was accentuated on the bare plot and monocultures located on the less fertile of our two soils (Table 4, Fig. 3), where acid saturation rose dramatically and exchangeable Al reached levels toxic to many annual crops (Spain et al. 1975).

The huge increases in extractable P we observed during the first 8 mo following clearing, followed by gradual decreases to values near the initial conditions within 2 yr (Fig. 2), are unlike any reports in the literature. Reports of increases in extractable P immediately after forest clearing and burning are commonplace (Jordan 1985), but long intervals between soil sampling may have caused other investigators to miss this dramatic phenomenon. Alternatively, the increase may be related to the unusual organic matter and N dynamics of our soil and may not occur on other tropical soils.

We suggest that the early increases in extractable P were related to changes in N mineralization and immobilization, both of which decreased ≈ 3 mo prior to the peak in extractable P shown in Fig. 7 (Matson et al. 1987). Microbes may have initially thrived on the P liberated during the burn, but soon became limited by a supply of readily mineralizable N. The P bound in microbial biomass may then have been released, resulting in the observed increases in extractable P. The subsequent decrease in P was probably the combined result of plant uptake and P fixation. The absence of uptake by plants in the bare plot probably resulted in the high values observed there.

Sulfur is potentially limiting for plant growth, especially in tropical areas where burning is a routine method of agricultural site preparation. Furthermore,

many tropical soils have high capacity to fix S (Bor-nemisza and Llanos 1967, Fox 1974, Sanchez 1976). The values for phosphate-extractable S at our site were low, but higher than the 8–10 mg/kg said to be critical for crop production on volcanic soils in Hawaii (Hasan et al. 1970). Even though substantial amounts of S were lost during our site-preparation burn (Ewel et al. 1981), extractable S increased early in the study and remained relatively constant thereafter. In vegetated plots, where significant amounts of S were taken up by plants, this constancy must have resulted from trapping atmospheric-S inputs ($\approx 0.9 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at our site, Hendry et al. [1984]) or from replenishment by S mineralization (which can be high in tropical soils, e.g., Mueller-Harvey et al. 1985).

Cation retention.—Concentrations of extractable cations in our soils were similar to those of other moderately fertile soils of the humid tropics (e.g., Ghana [Greenland and Kowal 1960] and Peru [Stark 1971]). They were considerably higher than those reported for Spodosols in Venezuela (Herrera 1979), for laterites and sands in Surinam and Brazil (Stark 1970), or for Peruvian Ultisols (Sanchez et al. 1983), but were lower than those reported for alluvium in Guatemala (Snedaker and Gamble 1969) and upland soils of New Guinea (Edwards and Grubb 1982) and India (Toky and Ramakrishnan 1983).

Land-use history may be responsible for the fertility differences across the study-site soils. Most of the study area was a coffee plantation, abandoned nearly 80 yr ago, but the poorer of the two soils is close to an area that was once a pasture dominated by *Panicum maximum* Jacq.; the pasture probably once extended onto part of our study site. Occupancy by pasture may have resulted in nutrient loss that is still evident in the differences between the more fertile and less fertile soils of the study site. It is interesting, for example, that the initial values for extractable Mg (Fig. 5) and acid saturation (Fig. 6) in the poorer soil coincide almost exactly with the terminal values for the better soil; the same is true for CEC_c and Ca (not illustrated).

This hypothesis on the sensitivity of our volcanic soil to land-use practices differs from the findings of Juo and Lal (1977), who worked on an Alfisol in Nigeria and found that soil K increased under *Panicum maximum* but remained constant under forest fallow. Also, Buschbacher et al. (1988), who worked on a relatively nutrient-poor Oxisol in Brazil, reported that soil-nutrient concentrations after 3–8 yr were relatively independent of pasture-management intensity. They attribute this, in part, to greater uptake by the more luxuriant vegetation that grew on less intensely used sites.

What about the striking increase in extractable K we observed ≈ 1 yr after the start of the study (Figs. 4 and 7)? Reanalyses convinced us that it was not due to a consistent analytical error in the > 100 samples taken on that date. Dramatic changes in K are well docu-

mented in the literature and apparently are related to soil water content at the time of sampling (Leubs et al. 1956). Although the mechanism whereby moisture affects the change of K from extractable to unextractable forms is unknown, the effect differs as a function of mineralogy (Black 1968). The peak in K availability at 1 yr was preceded by peaks in nitrate-N and P (Fig. 7), which may have been related to microbial activity. The soil samples that were extremely high in exchangeable K were taken in March 1980, at the height of the dry season. If the K that becomes extractable in the dry season remains in that form after the start of the rainy season, it could be leached or readily taken up by plants.

If CEC_e were the only factor involved in cation retention in the soil, we would have expected the degree of retention to follow the lyotropic series: $Ca > Mg > K$. However, Mg depletion occurred more rapidly than that of either Ca (as expected) or K (not expected). One possible interpretation is that Mg was not actually removed, but that our soil immobilizes K. While the average Mg loss rates of $14\text{--}26\text{ mg}\cdot\text{kg}^{-1}\cdot\text{yr}^{-1}$ are comparable to other reports (e.g., Sanchez 1976, Toky and Ramakrishnan 1983), the sparse literature on depletion rates is inconclusive due to differences in methodologies. It is likely that the Mg losses were due primarily to leaching or immobilization rather than plant uptake, because the bare plot lost more than the vegetated plots.

As the base-forming cations (K, Ca, and Mg) decreased and exchange sites became increasingly occupied by acid-forming cations (H and Al), the soil lost some of its buffering capacity and soil pH decreased (see Ulrich 1981). With time, however, soil pH increased slightly, even in the bare plot. This increase in pH cannot be attributed to inputs of base-forming elements because concentrations in bulk precipitation at our site were very low (Hendry et al. 1984). The increase may be related to the great buffering capacity of allophane (Uehara and Gillman 1981), but we do not know what mechanism might translate this buffering capacity into an increase in pH.

Effects of plant communities

Two factors, organic matter and roots, play key roles in nutrient retention. Both of these can be manipulated by changing vegetation composition and turnover.

Organic matter was undoubtedly responsible for much of the CEC_e in our variable-charge soil, but its effect on CEC_e was more pronounced in the less fertile soil. In the more fertile soil there was no discernible change in CEC_e beneath the diverse communities, whereas CEC_e declined beneath both floristically simple and diverse communities on the less fertile soil. Loss of CEC_e , in turn, resulted in a release of cations. This then led to a decline in extractable cation concentrations during the 5-yr study. The implications of this chain of events are that the loss of cations can be

reversed only when CEC_e is restored, and this restoration is likely to be accomplished most readily by restoring soil organic matter. This was verified on some of our plots occupied by diverse vegetation where, when soil organic matter approached steady-state levels, the concentrations of extractable cations also stabilized.

The impacts of organic matter were most dramatic in the bare plot, where nutrient changes were far greater than those in any of the vegetated plots (including the monocultures). Without nutrient return to the surface as litter, fresh organic matter for soil microbes, and protective cover, the bare soil became so impoverished that few plants colonized towards the end of the study, despite a continuous rain of seeds from surrounding vegetation (Young et al. 1987).

Of the four kinds of vegetated plots, the monocultures underwent the greatest depletions of soil nutrients, as had been expected. Far more important from an agricultural perspective were the dramatic differences among the four monocultures. Soil nutrient depletion was greatest under the shortest lived monocultures (two maize crops of ≈ 100 d each), intermediate under the cassava (with an age at harvest of just over a year), and very modest under the *Cordia alliodora* trees, which occupied our monocultures for 3.5 yr.

These differences among the monocultures were probably due in large part to differences in root systems. The rapid turnover of a short-lived crop mitigates against development of an extensive root system, whereas the longevity of a perennial affords an opportunity to thoroughly exploit the soil and retain nutrients by plant uptake. Our *Cordia alliodora* monocultures, for example, had fine-root systems as extensive as those of the far more diverse 5-yr-old communities after only 3.5 yr (Berish and Ewel 1988). The maintenance of soil fertility is certainly one of the factors responsible for the fact that most demonstrably sustainable crops of the humid tropics, banana, cocoa, oil palm, rubber, are perennials (see Holdridge 1959, Alvim 1981, Ewel 1986).

Despite the potential for a monoculture, particularly one comprised of a perennial plant, to retain nutrients and maintain site quality, there is invariably a substantial risk involved. If patches of plants within a monospecific planting fail, some of the soil will be exposed and vulnerable to nutrient loss. Species richness provides insurance against such failure, for if one species fails another is present to occupy the void.

Did the addition of more species to the already species-rich successional community further enhance nutrient retentiveness? No. Even though the regular addition of copious quantities of seeds of extraneous species did augment diversity by $\approx 25\%$, it did not have significant effects on site quality.

Two of the species-rich communities, successional vegetation and the imitation of succession, had no species in common, yet they did not differ with respect to their impacts on soil fertility. No doubt the presence

or absence of particular species leads to small-scale spatial heterogeneity within such plots, but the ecosystem-level effects were indifferent to the species mix. Similar soil-nutrient dynamics can be achieved by both successional vegetation and human-built mimics of that vegetation. The implications of this finding for agroecosystem design and restoration are immense: create the structure and nutrient retention will follow. This opens the way for substitution of species that are particularly desirable, from economic, conservation, or aesthetic perspectives, into complex systems, preexisting or restored.

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