NUTRIENT CYCLING IN MOIST TROPICAL FOREST

P. M. Vitousek and R. L. Sanford, Jr.

Department of Biological Sciences, Stanford University, Stanford, California 94305

INTRODUCTION

Early studies of nutrient cycling in moist tropical forests described productive forests rich in nutrients (98, 114, 176) in which rates of primary production and the amounts of nutrients cycled clearly exceeded those in temperate zone forests. Reviews of global-scale patterns in biomass, production, and nutrient cycling reported these results as representative of tropical forests (130, 175). At the same time, tropical forest soils were described as acid, infertile clays that harden irreversibly to "laterite" when cleared (106), or as bleached quartz sands low in mineral nutrients (88). This apparent paradox was crystallized by Whittaker (174) in the statement "The tropical rain forest thus has a relatively rich nutrient economy perched on a nutrient-poor substrate" (p. 271).

Reviews of more recent research on overall patterns of mineral cycling in the tropics (78, 124), and of important components such as biomass (20, 21), litterfall nutrients (123, 164), and decomposition (5), clearly show that patterns of nutrient cycling in tropical forests are diverse. It makes no more sense to describe a 'typical' tropical forest than a 'typical' temperate forest (33, 151). Variations in mineral cycling nonetheless follow coherent, explicable patterns in tropical forests. Our purposes in undertaking this review are: (a) to illustrate the patterns of nutrient cycling in moist tropical forests; (b) to identify the mechanisms which regulate those patterns; and (c) to show how those patterns affect the productivity, physiology, and population biology of tropical forests and their large-scale linkages with aquatic ecosystems and the atmosphere. We emphasize the cycling of nitrogen, phosphorus, potassium, calcium, and magnesium; these are the best-studied soil-derived nutrients, and they are the nutrients most likely to limit primary production and other ecosystem functions.

137

APPROACH

The major factors underlying variations in nutrient cycling in forest ecosystems are climate (160), species composition, successional status (time since disturbance) (14, 166), and soil fertility (82, 163). For the purpose of this review, we define moist tropical forests broadly to include all forests between the Tropics of Cancer and Capricorn (23° 28' north and south) with average annual precipitation in excess of 1500 mm, and with a dry season (< 100 mm/month) of 4 months or less. By confining our analysis to moist forests, we avoid much of the climatically controlled diversity within the tropics. Nevertheless, a great deal of variation is related to the length and intensity of dry seasons (108) and to altitudinal gradients in tropical mountains (57). Variations in nutrient cycling due to the effects of species composition are difficult to isolate without the use of controlled experiments. These exist in tree plantations (138) but rarely in natural ecosystems; they are not considered here. Numerous studies have examined nutrient cycling in secondary succession, especially in relation to shifting cultivation, and that literature is discussed elsewhere in this volume (34).

We emphasize the relationship between soil fertility and nutrient cycling in this review. Our approach is to classify sites into groups of soils that differ in fertility and then to examine patterns of nutrient distribution, cycling, and loss in forests on these groups of soils. A number of different ways to classify soils are used in the tropics; we follow the US Soil Taxonomy System (159). This system is compared with the other major approaches in Sanchez (135) and Sombroek (145).

The areal extent of different soils in the moist lowland tropics is summarized in Table 1. Overall, oxisols and ultisols are the most common tropical soils, although they are less frequent in Asia than in Africa or the Neotropics (136). Oxisols and ultisols are rather broad categories, both of which have clays with low cation exchange capacity (kaolinite, aluminum and iron oxides), moderate to strong acidity, and low exchangeable cation content. They include soils that range from mildly to severely infertile (in terms of agricultural potential).

The 'alfisol and others' category (Table 1) includes a wide range of very different soils; their major common feature is moderate to high fertility. Such soils are more often found in regions with relatively low precipitation (1500–2000 mm) or with volcanic parent material, but small pockets of them are found intermingled with some of the least fertile oxisols and ultisols in the world (37). These soils are generally the most suitable for agricultural use, and the practice of establishing agricultural experiment stations on such soils can give a misleading picture of regional agricultural potential (37). We include all low-elevation volcanically derived and alluvial soils in this moderately fertile category.

Table 1 Proportional extent of major soils of the tropics. Sites with mean annual temperature >22°C, annual precipitation >1500 mm, and a dry season of less than 4 months/year are included.[a]

Soil and soil fertility class	Area (10^6 ha)	Percentage of area
Moderately to very low		
Oxisols	525	35.3
Ultisols	413	27.7
Moderately fertile		
Alfisols	53	3.6
Tropepts	94	6.3
Andepts	12	0.8
Mollisols	7	0.5
Fluvents	50	3.4
Vertisols	5	0.3
Other	2	0.1
Very low		
Spodosols	19	1.3
Psamments	90	6.0
Variable		
Aquepts	120	8.1
Low		
Lithic (shallow)	72	4.8
Histosols (organic)	27	1.8
Total	1489	

[a]From Sanchez (136).

Sandy soils of old river terraces and highly weathered upland sites make up the spodosol/psamments group. These soils support short, sclerophyllous vegetation; they often have a seasonally high water table and little if any agricultural potential. Their exceptionally low nutrient status has attracted a number of investigations, and some excellent research has resulted. However, the focus of nutrient cycling research on the extremely low-nutrient spodosol/psamment group on the one hand and the moderately high-nutrient alfisol group on the other has perhaps led to generalizations which exclude the more widespread oxisol/ultisol soils (138).

The poorly drained aquept soils (Table 1) include fertile soils in areas where sediment-laden floodwaters are deposited (e.g. the Mekong Delta, the *varzea* of Amazonia) and very infertile soils in regions flooded by blackwater rivers (e.g. the *igapo* of the Rio Negro) (142). The other groupings in Table 1

are less coherent (shallow soils) or less abundant (organic soils), and they are not considered further here.

The summary in Table 1 applies to lowland sites only. Moderately to highly fertile volcanically derived soils (andepts) and other geomorphologically young soils are more abundant at higher altitudes. At the same time, reduced temperatures in montane forests cause reduced rates of decomposition and nutrient release (57, 154). We treat these montane soils and the ecosystems they support as a distinct group, even though they involve a variety of soils.

We summarize patterns of nutrient cycling in forests on four major groups of soils—oxisols/ultisols, alfisols/other moderately fertile soils, spodosols/psamments, and montane. Our use of these relatively crude classes costs us some power in examining the effects of soil fertility—there are relatively fertile ultisols and relatively infertile alfisols. Nonetheless, we show that there are substantial differences in patterns of nutrient distribution and cycling among these groups of soils. This analysis can undoubtedly be refined when data relating measured soil properties on a site to nutrient cycling on that site are available. Currently, the data available for such an analysis across sites are sparse, and often the methods in use in different sites cannot be compared directly (78).

Nutrient Contents and Concentrations

Quantities of nutrients in aboveground biomass in a range of tropical forests are summarized in Table 2; root biomass and nutrient contents are discussed below. Total nutrient contents are determined by the amount of biomass, its distribution into different plant parts (leaves, branches, bark, boles), and the nutrient concentrations in each part. In addition, specialized groups such as epiphytes (111) and lianas (47, 153) can contribute substantially to the biomass and nutrient content of certain tropical forests.

Biomass does not differ strongly among sites with different soils in this limited sample, except that it is lower in the most infertile white-sand soils. Additional information on tropical forest biomass has been reviewed by Brown & Lugo (20), and further calculations based on the merchantable volume of forests are summarized in Brown & Lugo (21). Strong patterns relating soil fertility to biomass are not apparent in their analysis either. Total aboveground biomass is strongly dependent on stand age (successional status) as well as climate and soils. On average, forests on more fertile sites could be younger than those on infertile sites; shifting cultivators as well as modern agronomists recognize and utilize more fertile soils preferentially, and even natural forest turnover (by treefalls) may be more rapid on more fertile sites (162). Moreover, recent evidence shows that stand-level disturbance is widespread in tropical forests (46, 69, 140); many tropical forests that have long been considered 'virgin' or 'primary' are in fact successional. An association

Table 2   Above-ground biomass and nutrient content in a variety of moist tropical forests

Site	Biomass (T/ha)	Nutrient (kg/ha)					Reference
		N	P	K	Ca	Mg	
Moderately fertile soils							
Panama	316	—	158	3020	3900	403	(50)
Venezuela	402	1980	290	1820	3380	310	(60)
Ghana	233	1685	112	753	2370	320	(54, 114)
Infertile oxisols/utisols							
Ivory Coast-Banco	510	1400	100	600	1200	530	(11)
-Yapo	470	1000	70	350	1900	180	(11)
Brazil	406	2430	59	435	432	201	(91)
Venezuela	335	1084	40	302	260	69	(79, 80, 83)
Colombia-terrace	182	741	27	277	432	133	(41)
Spodosols/Psamments							
Venezuela-caatinga	185	336	32	321	239	53	(62 in 49)
-tall bana	180	618	62	669	568	200	(27)
-low bana	37	212	28	155	276	43	(27)
-open bana	5.5	32	2	29	24	7	(27)
Montane soils							
New Guinea	310	683	37	664	1281	185	(58)
Puerto Rico	197	814	43	517	894	340	(118)
Venezuela	348	876	53	1321	745	215	(55)
Jamaica-mull	337	857	41	829	940	193	(155)
-mor	209	426	30	272	353	155	(155)
Hawaii	176	367	28	380	756	72	(110)

between soil fertility and aboveground biomass is therefore unlikely in any but the most extreme cases.

Nutrient concentrations in individual tissues are more likely to reflect the influence of soil fertility. All leaves have the same basic function, and all utilize the same suite of nutrients in the process of fixing energy into organic forms. Data on the extent to which plants on different sites accumulate nutrients in leaves can thus be useful in comparing nutrient status in different species and sites (161). Moreover, the photosynthetic capacity of leaves is strongly correlated with leaf nutrient (especially nitrogen) concentrations (112), and the physiological mechanism for this correlation is well understood (39).

Nutrients in leaves can be expressed on the basis of leaf area or leaf weight. Nutrient concentrations in leaves (by weight) are sensitive to variations in the relative amounts of different tissues within leaves (57); the presence

of low-nutrient structural material within sclerophyllous leaves dilutes nutrient contents and yields lower concentrations. Leaves may be sclerophyllous as an adaptation to low water availability, low nutrient availability, or to high herbivore pressures (24, 121, 143), but if they are sclerophyllous for *any* reason, they will have low nutrient concentrations. When nutrients in sclerophyllous leaves are expressed on a leaf-area basis, they often equal or exceed nutrients in less sclerophyllous leaves (107).

Nutrient concentrations in the leaves of a number of tropical forests are summarized in Table 3. These results generally represent arithmetic mean concentrations of species on each site; geometric means (weighted for species abundance) would usually be lower (155).

Concentrations of all of the major nutrients in leaves are significantly elevated on the more fertile tropical soils (Table 3). The infertile oxisols/ultisols have intermediate nitrogen and low phosphorus and calcium concentrations—the calcium concentrations in two sites are the lowest that we have encountered anywhere. Sandy soils support vegetation with low foliar nitrogen and phosphorus, intermediate major cation concentrations, and high specific leaf weights (94, 107). In three side-by-side comparisons of oxisols with spodosols (93, 107), leaves on the oxisols always had higher nitrogen but lower potassium concentrations than did leaves on the sandy soils. Inundation forests in Amazonia which receive mineral-laden whitewater *(varzea)* have higher foliar P and cation concentrations than blackwater areas *(igapo)* (95a). Montane forest leaves generally have lower nutrient concentrations than those from fertile lowland forests, even though many are located on what would be classified as fertile soils in the lowlands (58, 155).

Nitrogen, phosphorus, and calcium concentrations of leaves from lowland forests are plotted against each other in Figure 1. Results from the major groups of soils clearly cluster into distinct areas of this figure, with the oxisol/ultisol sites substantially higher in nitrogen than the spodosol soils.

The between-site variation in Table 3 and Figure 1 includes both the foliar chemistry of different species and the fertility of different soils. Where a single species is found on two sites that differ in soil fertility, foliar nutrient concentrations are usually quite similar (153), deviating only slightly in the direction of the mean difference between sites.

Nutrient concentrations in other plant parts have not been analyzed as often as leaves, although a number of useful summaries are available (51, 52, 95, 146). Where nutrient concentrations in leaves are correlated with nutrient concentrations in other plant parts, then foliar chemistry represents a useful indicator of overall nutrient status. Grubb & Edwards (58) and Tanner (155) examined these correlations in detail within particular sites; the latter found significant correlations for nitrogen and phosphorus while the former did not. Across the broader range of sites discussed here (Table 2, Table 3), foliar and overall nutrient concentrations are clearly positively correlated.

Table 3   Foliar nutrient concentrations in a range of moist tropical forests

Site	Nutrients (%)					Reference
	N	P	K	Ca	Mg	
Moderately fertile soils						
Panama	—	0.15	1.53	2.29	0.26	(50)
Ghana	2.52	0.14	0.85	1.54	0.48	(54, 113)
Venezuela	2.54	0.15	1.52	1.50	0.48	(60)
New Britain	2.08	0.15	1.67	2.04	0.30	(57)
Zaire	2.45	0.12	1.92	0.70	0.88	(8, 97)
Infertile oxisol/ultisol						
Venezuela	1.27	0.06	0.46	0.19	0.10	(107)
Venezuela	1.78	0.06	0.38	0.11	0.11	(93)
Brazil	1.84	0.05	0.50	0.42	0.29	(93)
Colombia-terrace	1.93	0.07	0.54	0.50	0.22	(41)
Spodosols/Psamments						
Venezuela-caatinga[a]	1.16	0.07	0.62	0.44	0.15	(107)
-caatinga[a]	1.08	0.06	0.58	0.53	0.36	(93)
-bana[b]	0.74	0.05	0.64	0.58	0.14	(107)
-tall bana[b]	1.03	0.09	0.68	0.46	0.26	(27)
-low bana[b]	1.29	0.12	0.72	1.03	0.25	(27)
-open bana[b]	0.89	0.04	0.55	0.64	0.22	(27)
Brazil-campina[c]	1.11	0.05	0.66	0.37	0.26	(94)
Malaysia	0.87	0.02	0.35	0.75	0.20	(121)
Montane sites						
Venezuela-cloud forest	1.17	0.08	0.55	0.87	0.26	(107)
-montane forest	1.74	0.08	0.66	0.64	0.23	(36)
Puerto Rico-lower montane	1.36	0.05	0.48	0.63	0.17	(107)
-elfin forest	0.99	0.06	0.51	0.67	0.16	(107)
New Guinea-lower montane	1.21	0.08	0.61	1.14	0.25	(58)
Hawaii	0.61	0.08	0.61	0.79	0.18	(110)
Jamaica-mull	1.78	0.08	1.17	1.0	0.46	(155)
-mor	1.11	0.06	0.43	0.80	0.33	(155)

[a]Sandy soil, occasionally flooded, tall vegetation.
[b]Sandy soil on higher ground, seasonally high water table lower-stature vegetation.
[c]Sandy soil on high ground; low-stature vegetation.

NUTRIENT TRANSFERS: PLANTS TO SOIL

Litterfall

More information is available to support generalizations about litterfall than
those about any other ecosystem-level aspect of tropical forests. Litterfall is
only one facet of nutrient cycling in forests, however, and not always the one
of greatest interest. Nonetheless, a knowledge of the amounts of nutrients
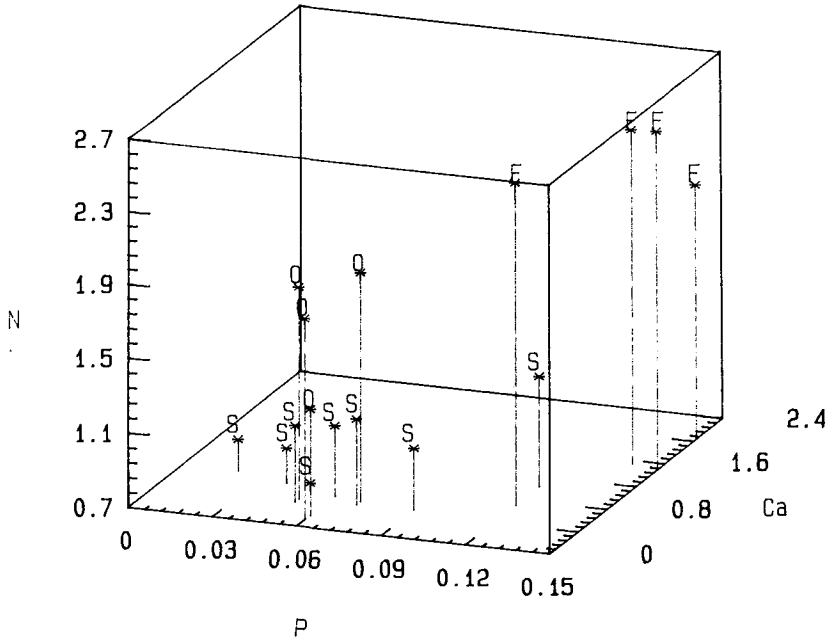
Figure 1 Foliar nitrogen, phosphorus, and calcium concentrations in lowland moist tropical forests; sources are in Table 3. "F" represents foliar concentrations in forests on alfisols or other moderately fertile soils, "O" represents oxisols/ultisols, and "S" represents spodosols/psamments.

cycled through litterfall can be most useful because litterfall represents a major process for transferring nutrients from aboveground vegetation to soils, and the relative rate at which forest vegetation loses organic matter versus particular nutrients provides an index of the efficiency of nutrient use within vegetation (64, 163).

Research on nutrients in tropical forest litterfall was reviewed recently by Proctor (123) and Vitousek (164). Sites drawn from those reviews that could be classified by soil types are summarized in Table 4; care was taken not to bias this sample by including within-study replicates of similar forest types. Several sites in Table 4 appear to represent intermediates between classes of soils. For example, litterfall in moderately fertile sites from Costa Rica, Guatemala, and Sarawak sites is relatively low in nutrients, while the "infertile" Ivory Coast and Colombia sites have relatively high nutrient concentrations. Where information is available, these same sites also appear as intermediates in Tables 2 and 3, contributing substantially to within-soilgroup variation. Nonetheless, it is clear that the forests on the moderately fertile soils return more litter at higher nutrient concentrations, and hence lower organic matter/nutrient ratios, than do forests on the other soils. In contrast, forests in the oxisol/ultisol group return smaller amounts of phos-

phorus and calcium at significantly higher dry mass/element ratios than do moderately fertile sites (t-test, $p < .05$), although their nitrogen levels are similar. Both of the spodosol sites cycle small quantities of nitrogen and phosphorus at low concentrations in litter. Direct comparisons of litterfall between nearby oxisol and spodosol sites in both Sarawak and Venezuela show that phosphorus is cycled more efficiently on the oxisols, but that nitrogen levels are extremely low on the spodosols (164). Finally, the montane sites are variable, but upper montane forests in general (the last 4–5 sites in Table 4) are low in both nitrogen and phosphorus. Only the spodosols and upper montane forests have elevated dry mass/nitrogen ratios in litterfall comparable to those in many temperate forests (163).

Patterns for nitrogen, phosphorus, and calcium concentrations in fine litterfall are summarized in Figure 2; the same groupings are observed as in Figure 1. To what extent can the withdrawal of nutrients prior to leaf abscission shape the pattern in Figure 2? Twigs, reproductive parts, and to some extent insect frass are included in Figure 2 but not in Figure 1, so no direct comparison is valid. We evaluated the importance of nutrient retranslocation by comparing nutrients in active leaves with nutrients in leaf litterfall (Table 5). Although these data are sparse and exclude the effects of
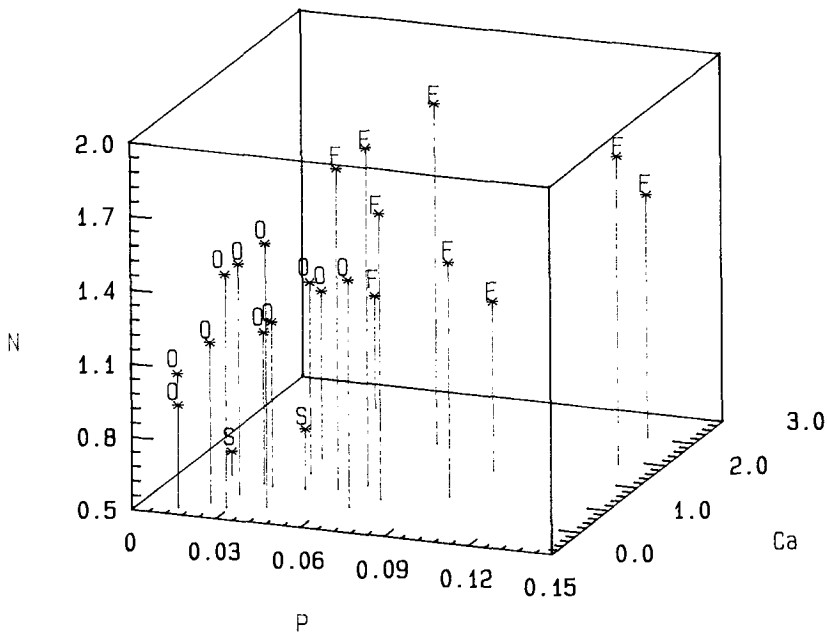

Figure 2   Concentrations of nitrogen, phosphorus, and calcium in the fine litterfall of moist lowland tropical forests; sources are in Table 4. "F" represents concentrations in forests on alfisols/other moderately fertile soils, "O" represents oxisols/ultisols, and "S" represents spodosols/psamments.

Table 4 Dry mass and nutrient content of fine litterfall in moist tropical forests.[a]

Site	Litterfall (T/ha)	Nutrients (kg/ha)					Reference
		N	P	K	Ca	Mg	
Moderately fertile soils							
Ghana	10.7	202	7.4	68	209	45	
Zaire	12.4	224	7.0	48	105	53	
Panama	11.4	—	9.4	29	256	34	
Panama	11.1	195	15.0	47	212	26	(99)
Costa Rica	8.1	135	6.0	20	59	16	(99)
Guatemala	9.0	169	5.8	20	88	64	
China	11.6	169	11.0	29	108	51	
Sarawak	11.5	110	4.1	26	290	20	
Australia	9.0	134	12.0	64	226	29	
Australia	10.4	124	10.2	56	159	36	
Mean (± S.D.)	10.5(1.4)	162(39)	8.8(3.3)	41(18)	171(78)	37(16)	
Mean dry mass/Element ratio (± SD)		67(17)	1370(604)	302(118)	76(37)	328(136)	
Infertile Oxisol/Ultisols							
Ivory Coast-Banco	11.9	170	8.0	28	61	51	
Ivory Coast-Yapo	9.6	123	4.0	26	105	23	
Colombia-terrace	12.0	141	4.2	17	90	20	
Colombia-slope	8.7	103	3.4	30	124	11	
Brazil	9.9	156	4.1	17	33	27	
Brazil	7.3	106	2.1	13	18	14	
Brazil	7.9	114	2.2	18	42	14	
Brazil	6.4	74	1.4	21	20	1	

Venezuela	5.8	61	0.8	6	8	4
Malaysia	8.9	100	2.8	32	70	18
Sarawak	8.8	81	1.2	33	13	9
Mean (± SD)	8.8(1.9)	108(38)	3.1(1.9)	22(8)	53(41)	17(13)
Mean dry mass/Element ratio (± SD)		82(13)	3740(1930)	472(218)	294(226)	1165(1768)
Spodosols/Psammments						
Venezuela	5.6	42	2.6	27	43	9
Sarawak	9.2	55	1.6	18	83	12
Mean	7.4	48	2.1	22	63	10
Mean dry mass/Element ratio		150	3950.0	359	120	694
Montane Forests						
Papua New Guinea	7.6	90	5.0	28	95	19
Venezuela	7.0	69	4.0	33	43	14
Puerto Rico	5.5	88	1.0	7	50	10
Philippines	5.3	89	4.8	16	61	9
Sarawak	11.0	86	2.5	31	21	16
Sarawak	3.6	28	1.1	6	6.5	6
Jamaica-mull	5.5	49	1.5	39	50	17
Jamaica-mor	6.6	39	1.3	15	34	19
Hawaii	5.2	37	2.1	12	84	10 (110)
Mean (± SD)	6.4(2.0)	64(25)	2.6(1.7)	21(11)	49(28)	13(5)
Mean dry mass/Element ratio (± SD)		110(36)	2850(1890)	397(199)	209(191)	502(123)

aInformation from Proctor (123) except where otherwise cited.

148   VITOUSEK & SANFORD

leaching (discussed below), the results clearly suggest that sites with high dry mass/nutrient ratios in litterfall also have high ratios (low nutrient concentrations) in active leaves.

Retranslocation of nutrients also appears to contribute to the pattern in Figure 2. Nutrient withdrawal from leaves cannot be calculated simply by comparing concentrations in leaf litter with those in leaves, because variable amounts of organic matter as well as nutrients are withdrawn prior to senescence. To overcome this problem, we assumed that calcium is immobile once it reaches leaves, and we estimated retranslocation by dividing the nutrient/Ca ratio in leaf litterfall by the nutrient/Ca ratio in leaves. Viewed in this way, phosphorus retranslocation appears to be greater in the infertile lowland tropical sites on oxisols or ultisols (where foliar P concentrations are already low) than in the one fertile site (Table 5). The pattern of efficient phosphorus utilization in infertile oxisol/ultisol sites (Figure 2) thus appears to be a con-

Table 5 Element concentrations in leaves and leaf litter, nitrogen to phosphorus ratios, and nitrogen and phosphorus retranslocation.[a]

Site	Elements (%)			N/P ratio	Retranslocation[a]		Reference
	N	P	Ca		N (%)	P (%)	
Moderately fertile							
Ghana leaves	2.52	0.14	1.54	18			
Leaf litter	2.1	0.09	2.0	23	36	51	(114)
Infertile Oxisol/Ultsol							
Colombia leaves	1.93	0.07	0.50	28			
Leaf litter	1.30	0.035	0.80	37	58	69	(40)
Venezuela leaves	1.78	0.06	0.11	30			
Leaf litter	1.59	0.03	0.17	53	42	67	(28)
Spodosols/Psamments							
Venezuela:							
Caatinga leaves	1.08	0.07	0.53	15			
Leaf litter	0.70	0.05	0.77	14	55	50	(28)
Open Bana leaves	0.89	0.04	0.64	22			
Leaf litter	0.58	0.02	0.74	29	44	56	(28)
Montane[b]							
Venezuela leaves	1.74	0.08	0.64	22			
Leaf litter	1.2	0.06	0.73	20	40	32	(36)
Papua New Guinea leaves	1.21	0.08	1.14	15			
Leaf litter	1.30	0.07	1.30	19	6	23	(58)

[a]Retranslocation calculated on the basis of element to calcium ratios in leaf litter versus leaves
[b]Also information in Tanner (155), but leaf Ca concentrations are greater than leaf litter Ca concentrations. This difference may reflect the use of arithmetic means for leaves and pooled samples (geometric means) for leaf litter.

sequence of both low foliar phosphorus concentrations and effective phosphorus retranslocation.

Throughfall

Throughfall and stemflow also return nutrients from vegetation to soil. Nutrients in stemflow are generally a small fraction (<10%) of those in throughfall in mature forests (119); stemflow is not considered further here. Nutrient transfers via throughfall were reviewed recently by Parker (119); his results and those of a few additional studies are summarized in Table 6. The values reported are net throughfall, defined as the amount of nutrients added to precipitation as it passes through the canopy.

The data in Table 6 are extremely sparse, but it is clear that throughfall is generally a relatively minor vector for nitrogen, phosphorus, and calcium transfer in tropical forests, although it is the major pathway of potassium transfer. These admittedly fragmentary results suggest that forests on mod-

Table 6 Net throughfall in moist tropical forests.*

Site	Nutrients (kg/ha)				Mg	Reference
	N	P	K	Ca		
Moderately fertile soils						
Australia	—	—	125	50	25	(18)
Australia	—	—	97	56	21	(18)
Ghana	13	3.7	220	29	18	
Panama	—	−0.5[c]	63	14	8	
Infertile Oxisol/Ultisols						
Ivory Coast	60	1.5	60	23	34	
Ivory Coast	13	5.5	82	19	41	
Malaysia	—	—	40	15	2	
Brazil	7.4[a,b]	.45[a]	20	1.0[b]	7.8[b]	(43)
Brazil	5.6[a,b]	.54[a]	13	7.2[b]	3.1[b]	(43)
Venezuela	4[a]	−14[a]	−6	−23	−2	
Spodosol/Psamment						
Venezuela	8[a]	−20[a]	4	−22	0.5	
Montane						
Papua New Guinea	30	2.5	71	19	11	(31)
Puerto Rico	—	—	74	21	29	
Venezuela	8	1.4	70	7	3	(56)

*Data is from review by Parker (119) unless otherwise cited.
[a]Only inorganic forms of this element included.
[b]Gross throughfall; element not detectable in incident precipitation.
[c]Negative values indicate net absorption in the forest canopy.

erately fertile soils lose more potassium and calcium via throughfall than do those on infertile sites, a pattern consistent with that observed in the temperate zone (156).

DECOMPOSITION AND NUTRIENT AVAILABILITY

The breakdown of litter and soil organic material releases nutrients into forms available to plants and microorganisms and thereby completes the nutrient cycle in forest ecosystems. We first examine decomposition and nutrient release from the surface litter layer, and then those processes in the more dispersed organic material within the soil.

Surface Litter

DECOMPOSITION   Rates of leaf litter decomposition in tropical forests were reviewed recently by Anderson & Swift (5). They examined decomposition in two ways: Litter turnover (k_L) was calculated as annual litterfall divided by litter standing crop on the soil surface, or alternatively, an exponential decay constant (k) was fitted to the rates at which confined leaves lose weight. These approaches often yield different results, in part because litter invertebrates (especially termites in many tropical forests) are generally excluded from confined leaves.

Anderson & Swift's (5) results demonstrate that rates of litter decomposition in tropical forests are variable, overlapping at their lower end with decomposition rates in temperate forests. These variations in decomposition rate appear to be broadly correlated with climate and soil fertility. Montane forests have distinctly lower rates of decomposition than do lowland forests (30, 154), as would be expected from the low montane temperatures. Values for k_L (litter layer turnover) overlap completely between moderately fertile sites and infertile oxisol/ultisol sites (5), but the litter layer is massive and k_L is small on spodosol/psamment sites. Measurements of weight loss of confined leaves also suggest that decomposition is slow on spodosols. Decomposition in a low-nutrient Venezuelan oxisol was relatively slow (k = 1.1), but decomposition in two adjacent spodosols was much slower (k = 0.34–0.42 on bana, 0.78 on caatinga) (27). Similarly, decomposition in a relatively fertile *varzea* floodplain forest (k = 1.08) exceeded that in an infertile *igapo* floodplain (0.48) (68). In contrast, surprisingly little variation in decomposition rate was observed among four contrasting sites in Sarawak (4), but nitrogen and phosphorus concentrations were relatively low and lignin extremely high in the litter of all four sites. Lignin concentrations correlate well with rates of decomposition in temperate forests (109).

NUTRIENT RELEASE   The general pattern of nutrient release from decomposing leaves in temperate and boreal forests involves the early immo-

bilization (net accumulation) of nitrogen and often phosphorus, followed by net nutrient release (16). A similar pattern of immobilization is observed (especially for phosphorus) in leaves from infertile tropical sites, but not those from fertile sites (4, 68, 97). Decomposers on infertile sites accumulate phosphorus from an extremely limited supply in the soil, so phosphorus immobilization probably places decomposers in competition with plants. This immobilization thus further reduces phosphorus availability.

Soil

DECOMPOSITION   Rates of organic matter decomposition within mineral soil are high in lowland moist tropical forests, a fact illustrated by the rapid disappearance of soil organic matter from land that has been cleared (115, 137). In contrast, montane tropical soils have larger amounts of soil organic matter that turns over slowly (3, 74), as do some volcanically derived soils in which allophane stabilizes soil organic matter (15, 144).

NITROGEN AVAILABILITY   Considerable information is available on the total quantities of nitrogen present in tropical soils (122), but it is difficult to relate this information to nitrogen availability to plants. The rate of conversion of organic nitrogen to biologically available ammonium and nitrate (mineralization) controls nitrogen availability in soils, but nitrogen mineralization has been measured in only a limited number of tropical forest soils. In comparison with rates in temperate forests, rates of nitrogen mineralization and nitrate production are rapid on alfisols and other fertile soils (29, 127, 165) and on oxisol/ultisols (11) in lowland sites. The only study on a spodosol (22) reported low rates of mineralization, and montane tropical soils also have relatively low mineralization (153, 167). These results are consistent with the high nitrogen concentrations and rapid circulation of nitrogen in vegetation in most lowland tropical sites (excepting spodosols) (Table 3, 4).

A close linkage between the decomposition of soil organic matter and nitrogen mineralization (104) may cause the rapid mineralization observed in most lowland tropical sites. Nitrogen is covalently bonded directly to carbon in soil organic matter, so rapid rates of decomposition imply rapid nitrogen release.

PHOSPHORUS AVAILABILITY   The phosphorus cycle in tropical soils is more complex than that of nitrogen. Ultimately, most phosphorus is derived from the chemical breakdown or weathering of parent material, and most of that original phosphorus can have been lost or become unavailable in the very old, highly weathered soils that characterize parts of the lowland tropics (66, 169). Additionally, phosphate (the biologically available form) is tightly adsorbed by a number of inorganic constituents of soils, including the sesquioxide clays

that characterize oxisols and ultisols (158) and allophane, in otherwise fertile young volcanic soils (35). Finally, most organic phosphorus in soils is not covalently bonded directly to carbon but rather is held by ester linkages which can be cleaved by extracellular phosphatases (104). Consequently, phosphorus in soils can cycle independently of the decomposition of organic matter.

The interaction of intensive, long-term weathering and rapid phosphorus adsorption by sesquioxides and allophane is probably ultimately responsible for the low availability, and hence the efficient cycling of phosphorus that is observed in oxisol/ultisol sites. Fertile soils generally have more total and available phosphorus (37), and inorganic phosphorus adsorption is generally less on soils of the spodosol/psamment group (103). Direct comparisons of phosphorus availability across sites are difficult, however, because all of the current methods yield only indexes of availability, and no single method is universally accepted.

CATIONS   Like phosphorus, the major cations are derived by weathering from parent material, and they are often present at very low levels in old, highly weathered soils. Cation adsorption is generally weaker than that of phosphorus, however, and "exchangeable" (salt-extractable) cations represent a reasonable estimate of instantaneous cation availability. Measurements of acid-extractable cations have been proposed as a means of estimating potential cation supply from weathering. Such measurements may correlate with plant species distributions better than do exchangeable cations in some situations (7). Extraordinarily small quantities of exchangeable calcium (5–7 kg/ha) are found within infertile oxisols in Amazonia (78) and Sarawak (125); these particular sites also have the lowest calcium concentrations in leaves and litter that have been observed anywhere (Tables 3, 4).

ROOT BIOMASS AND NUTRIENTS

Root production and nutrient cycling are difficult to study in any forest ecosystem, and our understanding of belowground processes has lagged well behind that of their aboveground counterparts. On the other hand, a considerable body of information has been collected on root biomass and its vertical distribution in soils (73, 126, 173); the existence of root mats above the soil surface in some tropical sites has been particularly well documented. Less information is available on nutrient contents of roots or nutrient turnover, however.

According to source-sink theory (12), trees should allocate more energy to roots on infertile sites, as this investment in nutrient acquisition should yield increased growth and/or reproduction in a nutrient-limited site. Consequently, greater root biomass and/or root-shoot ratios might be expected on less fertile soils (170). Comparisons of tropical forests within a region (13, 96) or across a wide range of sites (93) have indeed suggested elevated root/shoot ratios on

Table 7   Root biomass and nutrient content in moist tropical forest ecosystems for which root nutrient content is known. Aboveground biomass and nutrient content are included for comparison

Site		Biomass (T/ha)	Nutrients (kg/ha)					Reference
			N	P	K	Ca	Mg	
Moderately Fertile Soils								
Panama[a]	above	316	—	158	3020	3900	403	(50)
	below	11.2	—	6	81	208	27	
Ghana	above	233	1685	112	753	2370	320	(54)
	below	24.8	211	11	88	146	23	
Infertile Oxisols & Ultisols								
Brazil	above	406	2430	59	435	432	201	(89, 92)
	below	32.3	404	5	31	55	26	
Venezuela	above	335	1084	40	302	260	69	(80, 148)
	below	55.6	586	18.5	46	49	13	
Spodosols & Psamments								
Venezuela								
Caatinga	above	185	336	32	321	239	53	(62)
	below	132.2	834	69	327	244	142	
Tall Bana	above	180	618	62	669	568	200	(27)
	below	123.7	638	58	392	195	190	
Low Bana	above	37	212	28	155	276	43	(27)
	below	62.5	357	32	205	306	91	
Open Bana	above	5.5	32	2	29	24	7	(27)
	below	40.3	290	9	94	90	38	
Brazil								
Campina	below	29.5	270	6	26	53	33	(90)
Montane								
New Guinea[b]	above	310	683	37	664	1281	185	(32)
	below	28.0	120	5	150	314	51	
Venezuela	above	348	876	53	1321	745	215	(55)
	below	56.4	231	14	148	154	39	
Puerto Rico[a]	above	197	814	43	517	894	340	(118)
	below	78	300	16	230	300	85	
Jamaica (mull)	above	209	426	30	272	353	155	(155)
	below	53.7	92	3	49	165	38	

[a]Below-ground biomass underestimated.
[b]Does not include below-ground stumps.

nutrient-poor sites. However, the allocation of nutrients to roots versus shoots on fertile as opposed to infertile soils has not been as well documented. We summarize published information on root biomass and nutrient contents in Table 7; these are compared with aboveground biomass and nutrient content where data are available.

Table 7 includes relatively few sites other than spodosols, where sampling is easier and the root mat extremely well developed. Nonetheless, overall root biomass appears to be greatest on relatively infertile sites, and root/shoot ratios are clearly elevated in the spodosol/psamments as a group, particularly in the less productive of the spodosol/psamment sites (13). As is the case with aboveground tissues, concentrations of nutrients (amount divided by dry mass) are generally lower in roots on the infertile sites, and the oxisol/ultisol sites have higher nitrogen/phosphorus ratios than do the spodosols (Table 7). The overall pattern of aboveground vs belowground nutrient allocation is similar to that for dry mass.

The values in Table 7 represent total root biomass, including structural tissues as well as roots actively engaged in nutrient and water adsorption. Although there is no agreed-upon definition for the division of roots into functional categories, roots <6 mm in diameter have been considered as "fine roots", actively growing and absorbing nutrients. Root biomass and nutrient content for this "fine root" fraction is summarized in Table 8. Few data are available, but this limited evidence suggests that the biomass of functionally active fine roots is substantially greater on infertile sites. Fine root biomass may generally be less than leaf biomass on moderately fertile sites and greater on infertile sites. Fine roots have higher nitrogen concentrations and lower cation concentrations than larger roots (Tables 7, 8). Nutrient concentrations in fine roots are less than those in leaves, although the difference is surprisingly small for nitrogen and phosphorus in the less fertile sites.

Table 8   Biomass and nutrient content of fine (<6 mm diameter) roots in moist tropical forests

Site	Biomass (T/ha)	Nutrient (kg/ha)					Reference
		N	P	K	Ca	Mg	
Moderately fertile soils							
Ghana	4.99	68	4	28	44	5	(54)
Infertile Oxisols/Ultisols							
Brazil	14.57	146	2	10	16	9	(89, 92)
Spodosols/Psamments							
Venezuela	54.70	364	31	157	87	78	(62)
Brazil	15.91	170	5	17	19	24	(90)
Montane							
New Guinea[a]	2.80	21	1	11	20	17	(32)
Venezuela[a]	24.60	157	9	58	108	25	(55)

[a]Includes roots <5 mm in diameter only.

The turnover of fine roots ("root production") is extremely difficult to measure, and the different methodologies used in temperate-zone forests yield widely differing results (1, 87, 168). Not surprisingly, little information on fine root turnover in humid tropical forests is available, and much of that is open to question. Root production has been estimated by measuring root ingrowth rates (27a, 62, 81), but the times over which ingrowth was measured were exceptionally long [>1 yr in (81)]. Using sequential cores and monthly observations on plexiglass windows, Sanford (139) estimated the turnover of roots less than 2 mm in diameter. Fine root turnover in the upper 10 cm of a Venezuelan oxisol was 25% per month; it yielded an annual fine-root production of 15.4 T ha^{-1} for this size and depth class of roots alone. Assuming that nutrients are *not* retranslocated from fine roots before they are sloughed, the amount of nutrients added to the soil by root turnover can be calculated as root mortality times nutrient concentration. Nitrogen and phosphorus concentrations in roots less than 2 mm in diameter at Sanford's site were 2.23% and 0.073% respectively (R. L. Sanford, unpublished), so the quantities of nitrogen and phosphorus added to the soil by turnover of these roots were 343 kg ha^{-1} yr^{-1} and 11 kg ha^{-1} yr^{-1} respectively. These compare to 61 and 0.8 kg ha^{-1} yr^{-1}, respectively, added by fine litterfall at this site (C. F. Jordan, personal communication) (Table 4).

These calculations could overstate the importance of root turnover if nutrients are retranslocated prior to root death, but they also understate turnover in that only 43% of the fine root mass was in the upper 10 cm of soil. We believe that research on root turnover and nutrient cycling in fertile vs infertile sites could greatly expand our view of nutrient cycling in moist tropical forests.

The turnover of mycorrhizal hyphae in the soil could also contribute to nutrient cycling in tropical soils, but the magnitude of this flux is unknown. Mycorrhizae are essential to the growth and survival of many tropical trees (70, 71), and it appears that different types of mycorrhizae are found on different tropical soils (150). It has been suggested that tropical mycorrhizae may transfer nutrients from litter directly to roots (172). In fact, surface root mats in spodosol/psamment sites do retain labelled calcium and phosphorus efficiently (147), and mycorrhizae in root mats can transfer labelled phosphorus from decomposing leaves to roots (63). However, there is no evidence that the mycorrhizae of trees actually decompose litter, and evidence is accumulating that the most abundant tropical mycorrhizae (vesicular-arbuscular mycorrhizae, or VAM) lack the enzymes necessary for decomposition (71). Nevertheless, the intimate contact between mycorrhizae and decomposing leaves in the forest floor is undoubtedly important to the phosphorus economy of many tropical (and temperate) plants (70).

SOIL FERTILITY AND NUTRIENT CYCLING: IMPLICATIONS

The results in Tables 1–8 clearly demonstrate that patterns of nutrient cycling differ in sites differing in soil fertility. Jordan & Herrera (82) suggested that forests could be viewed as representing a continuum from oligotrophic to eutrophic, and Jordan (78) arrayed a range of tropical sites on such a gradient. Our results suggest that a single gradient may not be sufficient because sites can be infertile in very different ways. The most extreme oxisol/ultisols are extraordinarily low in phosphorus and calcium, while the spodosols and upper montane sites (although different from each other) are both low in nitrogen.

Tropical forests on infertile sites display a combination of characteristics, including high root/shoot ratios, sclerophyllous leaves, low nutrient concentrations, and efficient nutrient cycling, that are generally associated with nutrient limitation in forest ecosystems (23). However, there are few direct measurements of changes in overall productivity following nutrient additions. The productivity of some mangrove stands increases in response to nitrogen fertilization (17), a result consistent with the high ratio of dry-mass to nitrogen in mangrove litter (2, 117 in 123). Similarly, application of a complete fertilizer caused increased tree growth on low-nutrient upper montane sites in Hawaii (48). We are not aware of any published fertilizer studies reporting changes in overall productivity in intact lowland rain forest; we would be most interested to learn whether productivity in oxisol sites responds to added phosphorus and/or calcium, spodosol/psamment sites to nitrogen and/or phosphorus, and upper montane sites to nitrogen.

Other Levels of Biological Organization

The patterns of nutrient cycling summarized here have a number of implications for the physiology (82, 107), community ecology (65), and plant population biology (25) of tropical forests. Reciprocal influences on patterns of nutrient cycling are equally likely. For example, palms and palm litter are rich in potassium (41), and palms could maintain large quantities of this element in circulation within tropical forests. Certain tree ferns may be similarly important for nitrogen; Mueller-Dombois et al (110) observed that the tree ferns accounted for 28% of the biomass, but 70% of the nitrogen, in a Hawaiian montane rain forest.

Patterns of nutrient allocation and cycling could also affect animal populations. Leaves on low-nutrient sites have elevated concentrations of fibrous and phenolic compounds that are thought to deter herbivory (105, 171). Several mechanisms could contribute to increased concentrations of these carbon-rich compounds on infertile sites (24, 38, 72); in addition low foliar nutrient levels may contribute directly to reducing herbivory. Irmler &

Furch (67) pointed out that a litter-feeding cockroach in Amazonia would need to consume impossible amounts (30–40 times its energy requirement) of litter to satisfy its phosphorus requirement; it could only maintain itself by consuming dead animals (which themselves when alive obtained phosphorus with difficulty) as well as litter. Similarly, folivores may satisfy their sodium nutrient requirements only by consuming soil or water plants (116). This low nutrient quality (as well as the low carbon quality) of leaves on infertile sites could reduce overall rates of consumption.

Animal activity can also affect pathways of nutrient cycling directly and indirectly. Haines (59) documented one direct effect—nests of *Atta* ants caused increased nutrient concentrations in the soil solution of an infertile oxisol. An indirect effect of animals (on a large scale) may be the selective pressure they exert on the secondary compounds of plants. Such compounds may retard decomposition and nutrient release (4) as well as deter grazers.

Input-Output Budgets

The distribution and cycling of elements in tropical forests takes place within the context of inputs by means of precipitation, mineral weathering, and gas absorption (including biological nitrogen fixation), and of outputs by means of solution losses (leaching) and volatilization. In the short run, nutrient availability is regulated by the balance between processes releasing nutrients into available forms and those removing them; in the longer run, the nutrient status of a forest ecosystem is dependent on the balance between inputs and outputs of nutrients.

INPUTS   The nutrient content of rainfall has been measured in a number of tropical sites, and results of these studies are summarized in Table 9. These studies all include nutrients dissolved in precipitation, but the deposition of aerosols on vegetation is excluded due to the limited amount of information currently available on aerosol chemistry in tropical areas (6, 141).

Most of the results in Table 9 are within the range of results in many temperate sites. There is a trend towards somewhat higher annual cation deposition in the more seasonal sites (Ghana, Ivory Coast, Panama), and this pattern is more pronounced when drier forests and savannas are included (85). The lowland Venezuelan site in Table 9 reported very high deposition of nutrients, especially phosphorus (77), but we believe the phosphorus results are in error. A few measurements by Galloway et al (45) on the same site yielded much lower estimates of deposition, ones that are more consistent with other tropical and temperate sites.

The chemical weathering of minerals adds phosphorus, potassium, calcium, magnesium, and most other nutrients to forests. Newly deposited or uplifted material usually weathers rapidly, but rates decline with time because

Table 9 Precipitation inputs of elements in moist tropical forests

| Site | Nutrients (kg/ha/yr) | | | | | Reference |
	N	P	K	Ca	Mg	
Ghana	14	0.12	17.5	12.7	11.3	
Ivory Coast	21.2	2.3	5.5	30.0	7.0	
Camaroun	12	1.7	12.0	3.8	1.5	
Zaire	6.4		2.0	3.9	1.1	
Costa Rica	5	0.2	2.5	1.4	1.0	(61)
Costa Rica	1.7[a]	0.17[a]	5.4	3.1	2.6	(120)
Panama		1.0	9.5	29.3	4.9	
Puerto Rico	14			34.0	26.0	
Venezuela-lowland[b]	21[a]	25[a]	24.0	28.0	3.0	
-montane	9.9	1.1	2.6	5.6	5.2	
Brazil	10	0.3		3.7	3.0	
Brazil	6[a]	0.16[a]	3.4	ND[c]	ND[c]	(43)
Australia			4.0	3.0	2.5	
Malaya			12.5	14.0	3.0	
Malaya	13.5		6.4	4.2	0.7	
Papua New Guinea-lowland			0.8	0.0	0.3	
-montane	6.5	0.5	7.3	3.6	1.3	

[a]Inorganic forms of the element only.

[b]Wet and dry fall together. Galloway et al (1982) collected and analyzed 14 precipitation samples (wet-fall only) on the same site. Their volume weighted concentrations times an annual precipitation of 3500 mm yields annual deposition rates of 2.4^a kg/ha N, 0.65^a kg ha^{-1} P, 1.1 kg ha^{-1} K, 0.2 kg ha^{-1} Ca, and 0.2 kg ha^{-1} Mg.

[c]Not detectable. Below detection limits.

[d]Information was derived from Steinhardt & Fassbender (149) or Proctor (124) unless otherwise cited. Some of the studies report inorganic forms of N and P only, while others report total quantities.

only the more recalcitrant minerals remain in soil (53). Chemical weathering is rapid in the humid tropical climate; hence, weatherable minerals are lost early during soil development. Soils of many tropical areas are old (66, 145), and it is not surprising that many are now poor in nutrients.

Very little information is available on the inputs of most trace gases into tropical forests. In many cases appropriate methodologies for measuring those inputs are currently becoming available only in extremely well-instrumented sites (102). Biological nitrogen fixation has been widely studied within the tropics, although most effort has been directed towards cropping, fallow, or pastoral systems (34, 128). Sylvester-Bradley et al (152) estimated rates of symbiotic nitrogen fixation in major forest ecosystems of Amazonia; they suggested high rates (up to 200 kg ha^{-1} yr^{-1}) in fertile *varzea* floodplain forests, intermediate rates in moderately infertile ultisols (to 20 kg ha^{-1} yr^{-1}), and very low rates (ca 2 kg ha^{-1} yr^{-1}) in infertile oxisols. Legumes with the potential to form nitrogen-fixing symbiotic associations are widespread in many tropical forests, but their activity may be limited by the low availability of other nutrients (particularly phosphorus and calcium), or it may be repressed by the relatively high nitrogen availability in many tropical soils.

Nitrogen fixation has also been detected in a number of other organisms in tropical forests, including termites (9, 19), epiphylls (10), and epiphytic lichens (42). Fixation by these organisms contributes to their own nitrogen budgets, but its quantitative significance on an areal basis is unknown.

OUTPUTS   A number of studies have reported hydrologic outputs of nutrients from tropical forest ecosystems; these are summarized in Table 10. The sources and quality of data are mixed; calculations of outputs in some studies were based on the small watershed approach (101), in others on lysimeter measurements of solution concentrations coupled with careful hydrologic budgeting (120), and in still others on the less sophisticated lysimetric approaches. Each of these approaches has virtues, but comparability with different methods at other sites is not one of them. Several advances in techniques for estimating hydrologic losses have recently been applied in tropical forests; these include tracing water pathways and reservoirs using ^{18}O (100, 134) and partitioning channelized versus matrix flow of water and nutrients within soils (131). When these techniques are in widespread use, they will greatly increase our ability to compare nutrient outputs among sites.

No useful patterns can now be drawn from the results in Table 10. In part this reflects the mixture of techniques, which are designed to sample different fluxes. Additionally, phosphorus outputs from the lowland Venezuelan sites

Table 10   Hydrologic losses of elements in moist tropical forest ecosystems. Most values represent inorganic forms of the element only

Site	Nutrients (kg/ha/yr)					Reference
	N	P	K	Ca	Mg	
Moderately fertile						
Costa Rica[a]	19.4	0	3.6	5.7	8.5	(120)
Panama[b]	—	0.7	9.3	163.0	44.0	(50)
Papua New Guinea-lowland[b]	—	—	15.0	25.0	51.0	(157)
Oxisol/Ultisol						
Venezuela-lowland oxisol	—	30.0	4.6	3.9	0.7	(77)
Brazil[b]	0.2	0.008	0.4	ND[c]	ND[c]	(43)
Brazil		0.04	12.7	16.7	8.1	(132 in 138)
Malaysia	—	—	11.3	2.1	1.5	(86)
Spodosol/Psamment						
Venezuela	—	16.0	—	2.8	—	(62)
Montane						
Venezuela	5.0	0.3	2.2	1.6	0.6	(56)

[a]Budget over a 404-day period.
[b]Outputs sampled in streamwater; otherwise using lysimeters.
[c]Not detectable.

appear extraordinarily high. It is unlikely that large quantities of phosphorus would leach from one of the most phosphorus-deficient forests in the world (Tables 2, 3, 4, 7) into surface waters that are also extraordinarily low in phosphorus (44); more likely, the values summarized in Table 10 are in error. Nutrient losses are probably higher in more fertile sites, but long-term information on nutrient losses in more sites will be necessary before we will be able to discern patterns of loss. Further studies of the mechanisms regulating solution losses of nutrients (75, 76) would also be most useful.

Losses of biogenic trace gases are known even less well than hydrologic losses, but the information available suggests that tropical forests could be a major source on a global scale (26). Salati et al (133) and Robertson & Rosswall (129) both calculated large-scale regional nitrogen budgets. They concluded that denitrification (the reduction of nitrate to nitrogen gas) is quantitatively more important than regional hydrologic outputs in both Amazonia and West Africa. Direct measurements of denitrification within intact tropical forests are sparse (80), but some evidence suggests that nitrous oxide (N_2O) production may be substantially greater in tropical than in temperate forests (84). Recent estimates suggest losses of 1–2 kg N_2O-N ha^{-1} yr^{-1} for Amazonian oxisols (M. Keller, personal communication). This is a large flux relative to temperate forests, but a small fraction of the nitrogen circulated annually in most forests on oxisols (Table 4). Rapid nitrogen turnover within many tropical forests could also be associated with elevated ammonia and nitric oxide fluxes, although measurements of such fluxes are nearly or wholly lacking.

SUMMARY

The results summarized here clearly demonstrate that patterns of nutrient cycling differ in forests on different soils. Moderately fertile soils support productive forests that cycle large quantities of nutrient elements—results in keeping with earlier summaries (cf 130). In contrast, forests on the widespread oxisol/ultisol soils efficiently cycle smaller quantities of phosphorus and calcium, although they appear to be quite rich in nitrogen. Forests on sandy spodosol/psamment soils cycle small quantities of nitrogen (and in some cases phosphorus), and they have extraordinarily high root/shoot ratios. Finally, montane tropical forests in general appear to be low in nitrogen, and upper montane forests cycle substantially less nitrogen than do lower montane forests. These patterns affect the physiology, community ecology, and population biology of tropical forests. Research designed to investigate these interactions appears promising. Additionally, investigation of the regulation of belowground vs aboveground nutrient cycling and the regulation of atmospheric and hydrologic losses of elements from tropical forests are potentially productive lines of research.

ACKNOWLEDGMENTS

Literature Cited

1. Aber, J. D., Melillo, J. M., Nadelhoffer, K. J., McClaugherty, C. A., Pastor, J. 1985. Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: A comparison of two methods. *Oecologia* 66:317–21

2. Aksornkoae, S., Khenmark, C. 1980. Nutrient cycling in mangrove forests of Thailand. In *Asian Symposium on Mangrove Environment and Management*, pp. 1–14. Univ. Malaya, Kuala Lumpur, Malaya

3. Alexander, E. B., Pichott, J. 1979. Soil organic matter in relation to altitude in equatorial Colombia. *Turrialba* 29:183–88

4. Anderson, J. M., Proctor, J., Vallack, H. W. 1983. Ecological studies in four contrasting lowland rain forest in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter. *J. Ecol.* 71:503–27

5. Anderson, J. M., Swift, M. J. 1983. Decomposition in tropical forests. See Ref. 151, pp. 287–309

6. Artaxo Neto, P., Orsini, C. Q., Bouéres, L. C., Leslie, A. 1982. Aspectos estruturais do aerossol atmosférico da Bacia Amazônica. *Acta Amazon. (Suppl)* 12:39–46

7. Baillie, I. C., Ashton, P. S. 1983. Some soil aspects of the nutrient cycle in mixed dipterocarp forests in Sarawak. See Ref. 151, pp. 347–56

8. Bartholomew, W. V., Meyer, J., Laudelout, H. 1953. Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. *Ser. Sci. No. 57, Publ. L'Inst. Natl. L'Etude Agronom. Congo Belge*

9. Beneman, J. R. 1973. Nitrogen fixation in termites. *Science* 181:164–65

10. Bentley, B. L., Carpenter, E. J. 1980. Effects of desiccation and rehydration on nitrogen fixation by epiphylls in a tropical rainforest. *Microb. Ecol.* 6:109–13

11. Bernhard-Reversat, F. 1977. Recherches sur les variations stationelles des cycles biogéochemiques en forêt ombrophile de Côte d'Ivoire. *Cah. ORSTOM, Ser. Pedol.* 15:175–89

12. Bloom, A. J., Chapin, F. S. III, Mooney, H. A. 1985. Resource limitation in plants—an economic analogy. *Ann. Rev. Ecol. Syst.* 16:363–93

13. Bongers, F., Engelen, D., Klinge, H. 1985. Phytomass structure of natural plant communities on spodosols in southern Venezuela: The Bana woodland. *Vegetatio* 63:13–34

14. Bormann, F. H., Likens, G. E. 1979. *Pattern and Process in a Forested Ecosystem.* New York: Springer-Verlag

15. Bornemisza, E., Pineda, R. 1969. Minerales amorfos y mineralizacion de nitrogeno en suelos derivados de cenizas volcanicas. In *Suelos Derivados de Cenizas Volcanicas de America Latina*, pp. B.7.1–7. Turrialba, Costa Rica: FAO-IICA Symposium

16. Bosatta, E., Staaf H. 1982. The control of nitrogen turnover in forest litter. *Oikos* 39:143–51

17. Boto, K. G. 1983. Nutrient status and other soil factors affecting mangrove productivity in northeastern Australia. *Wetlands* (Australia) 3:45–50

18. Brassell, H. M., Sinclair, D. F. 1983. Elements returned to forest floor in two rainforest and three plantation plots in tropical Australia. *J. Ecol.* 71:367–78

19. Breznak, J. A., Brill, W. J., Mertins, J. W., Coppel, H. C. 1973. Nitrogen fixation in termites. *Nature* 244:577–80

20. Brown, S., Lugo, A. E. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161–87

21. Brown, S., Lugo, A. E. 1984. Biomass of tropical forests: A new estimate based

on forest volumes. *Science* 233:1290–93

22. Chandler, G. 1985. Mineralization and nitrification in three Malaysian forest soils. *Soil Biol. Biochem.* 17:347–53

23. Chapin, F. S. III, Vitousek, P. M., Van Cleve, K. 1986. The nature of nutrient limitation in plant communities. *Am. Nat.* 127:48–58

24. Coley, P. D., Bryant, J. P., Chapin, F. S. III. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–99

25. Cox, P. A. 1981. Niche partitioning between sexes of dioecious plants. *Am. Nat.* 117:295–307

26. Crutzen, P. J., Delany, A. C., Greenberg, J., Haagenson, P., Heidt, L., et al. 1985. Trospheric chemical composition measurements in Brazil during the dry season. *J. Atmos. Chem.* 2:233–56

27. Cuevas, E., Klinge, H. 1986. Bana: Biomass, nutrient content, litter fall, and decomposition. IVIC volume, San Carlos de Rio Negro Project. In press

27a. Cuevas, E., Medina, E. 1983. Root production and organic matter decomposition in a tierra firme forest of the upper Rio Negro Basin. In *Wurzelökologie und ihre Nutzanwendung,* pp. 653–66. Int. Symp. Gumpenstein 1982

28. Cuevas, E., Medina E. 1986. Nutrient dynamics in Amazonian forest ecosystems. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. *Oecologia.* 68:466–72

29. de Rham, P. 1970. L'azote dans quelques forêts, savanes, et terrains de culture d'Afrique tropicale humide. *Veröff. Geobot. Inst. Eidgenössische Tech. Huchschule Zurich* 45:

30. Edwards, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. II. The production and disappearance of litter. *J. Ecol.* 65:971–92

31. Edwards, P. J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall. *J. Ecol.* 70:807–27

32. Edwards, P. J., Grubb, P. J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil characteristics and the division of mineral elements between the vegetation and soil. *J. Ecol.* 70:649–66

33. Ewel, J. 1980. Tropical succession: Manifold routes to maturity. *Biotropica* 12(*Suppl.*):2–7

34. Ewel, J. J. 1986. Designing agroecosystems for the humid tropics. *Ann. Rev. Ecol. Syst.* 17:245–71

35. Fassbender, H. W. 1969. Deficiencia y fijacion de fosforo en suelos derivados

de cenizas volcanicas en America Central. See Ref. 15, pp. B.4.1–10

36. Fassbender, H. W., Grimm, V. 1981. Ciclós bioqúimicos en un ecosistema forestal de los Andes Occidentales de Venezuela. II. Producción y descomposición de los reśiduos vegetales. *Turrialba* 31:39–47

37. Fearnside, P. M. 1984. Initial soil quality conditions on the Transamazon highway of Brazil and their simulation in models for estimating human carrying capacity. *Trop. Ecol.* 25:1–21

38. Feeny, P. 1976. Plant apparency and chemical defense. In *Recent Advances in Phytochemistry,* Vol. 10, ed. J. W. Wallace, R. L. Mansell, pp. 1–40. NY: Plenum

39. Field, C., Mooney, H. A. 1986. The photosynthesis-nitrogen relationship in wild plants. In *On the Economy of Plant Form and Function,* ed. P. J. Givnish, pp. 25–55. Cambridge: Cambridge Univ. Press

40. Fölster, H., de las Salas, G. 1976. Litter fall and mineralization in three tropical evergreen stands, Venezuela. *Acta Cient. Venezolana* 27:196–202

41. Fölster, H., De las Salas, G., Khanna, P. 1976. A tropical evergreen forest site with perched water table, Magdalena Valley, Columbia. Biomass and bioelement inventory of primary and secondary vegetation. *Oecol. Plant.* 11:297–320

42. Forman, R. T. 1975. Canopy lichens with blue-green algae: A nitrogen source in a Colombian rain forest. *Ecology* 56:1176–84

43. Franken, W., Leopoldo, P. R. 1984. Hydrology of catchment areas of Central-Amazonian forest streams. See Ref. 142, pp. 501–19

44. Furch, K. 1984. Water chemistry of the Amazon Basin: The distribution of chemical elements among freshwaters. See Ref. 142, pp. 167–99

45. Galloway, J. N., Likens, G. E., Keene, W. C., Miller, J. N. 1982. The composition of precipitation in remote areas of the world. *J. Geophys. Res.* 87:8771–86

46. Garwood, N. C., Janos, D. P., Brokaw, N. 1979. Earthquake-caused landslides: A major disturbance to tropical forests. *Science* 205:997–99

47. Gentry, A. H. 1983. Lianas and the "paradox" of contrasting latitudinal gradients in wood and litter production. *Trop. Ecol.* 24:63–67

48. Gerrish, G., Bridges, K. W. 1984. *A thinning and fertilization experiment in* Metrosideros *dieback stands in Hawai'i.*

Hawaii Botanical Science Paper No. 43, Honolulu: Dep. Botany, Univ. Hawaii

49. Golley, F. B. 1983. Nutrient cycling and nutrient conservation. In *Tropical Rain Forest Ecosystems: Structure and Function,* ed. F. B. Golley, pp. 137–56. Amsterdam: Elsevier Scientific

50. Golley, F. B., McGinnis, J. T., Clements, R. G., Child, G. I., Deuver, M. J. 1975. *Mineral Cycling in a Tropical Forest Ecosystem.* Athens: Univ. Ga. Press

51. Golley, F. B., Yantko, J., Richardson, T., Klinge, H. 1980. Biogeochemistry of tropical forests. I. *Trop. Ecol.* 21:59–70

52. Golley, F. B., Yantko, J., Jordan, C. F. 1980. Biogeochemistry of tropical forests. II. *Trop. Ecol.* 21:71–80

53. Gorham, E., Vitousek, P. M., Reiners, W. A. 1979. The regulation of element budgets over the course of terrestrial ecosystem succession. *Ann. Rev. Ecol. Syst.* 10:53–84

54. Greenland, D. J., Kowal, J. M. L. 1960. Nutrient content of the moist tropical forest of Ghana. *Plant Soil* 12:154–73

55. Grimm, V., Fassbender, H. W. 1981. Cíclos bioquímicos en un ecosistema forestál de los Andes Occidentales de Venezuela. I. Inventario de las reservas orgánicas y minerales (N,P,K,Ca,Mg, Mn,Al,Na). *Turrialba* 31:27–37

56. Grimm, U., Fassbender, H. W. 1981. Cíclos bioquímicos en un ecosistema forestál de los Andes Occidentales de Venezuela. III. Ciclo hidrológico y translocación de elementos químicos con el água. *Turrialba* 31:89–99

57. Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains, with special reference to mineral nutrition. *Ann. Rev. Ecol. Syst.* 8:83–107

58. Grubb, P. J., Edwards, P. J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. III. The distribution of mineral elements in the aboveground material. *J. Ecol.* 70:623–48

59. Haines, B. 1983. Leafcutting ants bleed mineral elements out of rainforest in southern Venezuela. *Trop. Ecol.* 24:85–93

60. Hase, H., Fölster, H. 1982. Bioelement inventory of a tropical (semi-)evergreen seasonal forest on eutrophic alluvial soils, Western Llanos, Venezuela. *Acta Oecol., Oecol. Plant.* 3:331–46

61. Hendry, C. D., Berish, C. W., Edgerton, E. S. 1984. Precipitation chemistry at Turrialba, Costa Rica. *Water Resour. Res.* 20:1677–84

62. Herrera, R. A. 1979. *Nutrient distribution and cycling in an Amazon caatinga forest on Spodosols in southern Venezuela.* PhD thesis. Univ. Reading, England

63. Herrera, R., Merida, T., Stark, N., Jordan, C. 1978. Direct phosphorus transfer from leaf litter to roots. *Naturwissenschaften* 65:208–09

64. Hirose, T. 1975. Relations between turnover rate, resource utility, and structure of some plant populations: A study of the matter budgets. *J. Fac. Sci. Univ. Tokyo* III. XI(II):355–407

65. Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. *J. Biogeogr.* 7:147–57

66. Irion, G. 1978. Soil infertility in the Amazonian rain forest. *Naturwissenschaften* 65:515–519

67. Irmler, I., Furch, K. 1979. Production, energy, and nutrient turnover of the cockroach *Epilampra irmleri* Rocha e Silva & Aguiar in a central-Amazonian inundation forest. *Amazoniana* 6:497–520

68. Irmler, V., Furch, K. 1980. Weight, energy, and nutrient changes during decomposition of leaves in the emersion phase of Central-Amazonian inundation forests. *Pedobiologia* 20:118–30

69. IUCN. 1984. Kalimantan—biggest fire ever? *Int. Union Conserv. Nature Nat. Resour. Bull.* 15:7

70. Janos, D. P. 1980. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. *Ecology* 61:151–62

71. Janos, D. P. 1983. Tropical mycorrhizas, nutrient cycles, and plant growth. See Ref. 151, pp. 327–45

72. Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69–103

73. Jenik, J. 1978. Roots and root systems of tropical trees: Morphologic and ecologic aspects. In *Tropical Trees as Living Systems,* ed. M. H. Zimmerman, P. B. Tomlinson, pp. 323–49 Cambridge: Cambridge Univ. Press.

74. Jenny, H. 1950. Causes of the high nitrogen and organic matter content of certain tropical forest soils. *Soil Science* 69:63–69

75. Johnson, D. W., Cole, D. W., Gessel, S. P., Singer, M. J., Minden, R. V. 1977. Carbonic acid leaching in a tropical, temperate, subalpine, and northern forest soil. *Arct. Alp. Res.* 9:329–43

76. Johnson, D. W., Richter, D. D., Van Miegroet, H., Cole, D. W. 1983. Contributions of acid deposition and natural processes to cation leaching from forest

soils: A review. *Air Pollut. Control Assoc.* 33:1036–41

77. Jordan, C. F. 1982. The nutrient balance of an Amazonian rain forest. *Ecology* 63:647–54

78. Jordan, C. F. 1985. *Nutrient Cycling in Tropical Forest Ecosystems: Principles and Their Application in Management and Conservation.* Chichester: Wiley 179 pp

79. Deleted in proof

80. Jordan, C., Caskey, W., Escalante, G., Herrera, R., Montagnini, F., et al. 1982. The nitrogen cycle in a 'tierra firme' rain forest on oxisol in the Amazon Territory of Venezuela. *Plant Soil* 67:325–32

81. Jordan, C. F., Escalante, G. 1980. Root productivity in an Amazonian forest. *Ecology* 61:14–18

82. Jordan, C. F., Herrera, R. 1981. Tropical rain forests: are Nutrients really critical? *Am. Nat.* 117:167–80

83. Jordan, C. F., Uhl, C. 1978. Biomass of a 'tierra firme' forest of the Amazon Basin. *Oecol. Plant.* 13:387–400

84. Keller, M., Goreau, T. J., Wofsy, S. C., Kaplan, W. A., McElroy, M. B. 1983. Production of nitrous oxide and consumption of methane by forest soils. *Geophys. Res. Letters* 10:1156–59

85. Kellman, M., Hudson, J., Sanmugadas, K. 1982. Temporal variability in atmospheric nutrient influx to a tropical ecosystem. *Biotrop.* 14:1–9

86. Kenworthy, J. B. 1971. Water and nutrient cycling in a tropical rain forest. In *The Water Relations of Malesian forests.* Transact. First Aberdeen-Hull Symp. Malesian Ecol., ed. J. R. Flenly, pp. 49–59. Inst. Southeast Asian Biology, Aberdeen: Univ. Aberdeen

87. Keyes, M. R., Grier, C. C. 1981. Above- and below-ground net production in 40-yr-old Douglas-fir stands on high and low productivity sites. *Can. J. For. Res.* 11:599–605

88. Klinge, H. 1966. Verbreitung tropischer Tieflandspodsole. *Naturwissenschaften* 17:442–43

89. Klinge, H. 1973. Root mass estimation in lowland tropical rain forests of central Amazonian, Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. *Trop. Ecol.* 14:29–38

90. Klinge, H. 1975. Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil. III. Nutrients in fine roots from giant humus podzols. *Trop. Ecol.* 16:28–38

91. Klinge, H. 1976. Bilanzierung von Hauptnahrstoffen im Ökosystem tropis-

cher regenwald (Manaus)—vorlaufige daten. *Biogeographica* 7:59–76

92. Klinge, H. 1976. Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil. IV. Nutriénts in fine roots from latosols. *Trop. Ecol.* 17:79–88

93. Klinge, H. 1984. Lowland Amazon forests, bioelements and geochemistry. Proc. 1° Simpósio do Tropico Úmido, pp. 333–46. Belem, Brasil

94. Klinge, H. 1985. Foliar nutrient levels of native tree species from Central Amazonia. 2. Campina. *Amazoniana* 9:281–95

95. Klinge, H., Furch, K., Harms, E. 1984. Selected bioelements in bark and wood of native tree species from Central-Amazonian inundation forests. *Amazoniana* 9:105–17

95a. Klinge, H., Furch, K., Harms, E., Revilla, J. 1983. Foliar nutrient levels of native tree species from Central Amazonia. I. Inundation forests. *Amazoniana* 8:19–45

96. Klinge, H., Herrera, R. 1983. Phytomass structure of natural plant communities on spodosols in southern Venezuela: The tall Amazon Caatinga forest. *Vegetatio* 53:65–84

97. Laudelot, H. 1962. Dynamique des sols tropicaux et les differents systems de jachere. *UN-FAO Rep.* 126 pp

98. Laudelot, H., Meyer, J. 1954. Les cycles d'éléments minerales et de matière organique en forêt équatoriale Congolaise. *Fifth Int. Congr. Soil Science* II:267–72

99. Leigh, E. G., Windsor, D. M. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. In *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes,* ed. E. G. Leigh, A. S. Rand, D. M. Windsor, p. 111–21. Washington, DC: Smithsonian Inst.

100. Leopoldo, P., Matsui, E. Salati, E., Franken, W., Goes Ribiero, M. 1982. Composicão isotópica da água de chuva e da água do solo em floresta amazônica do tipo terra firme, região de Manaus. *Acta Amazonica Suppl.* 12:7–13

101. Likens, G. E., Bormann, F. H., Pierce, R. S., Eaton, J. S., Johnson, N. M. 1977. *Biogeochemistry of a Forested Ecosystem.* New York: Springer-Verlag

102. Lindberg, S. E., Lovett, G. M., Richter, D. D., Johnson, D. W. 1986. Atmospheric deposition and canopy interactions of major ions in a forest. *Science* 231:141–45

103. Lopes, A. S., Cox, F. R. 1979. Relacão

de caracteristicas fisicas, químicas e mineralógicas com fixacão de fosforo em solos sob cerrados. *R. bras. C. Solo* 3:82–88

104. McGill, W. B., Cole, C. V. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. *Geoderma* 26:267–86

105. McKey, D., Waterman, P. G., Gartlan, J. S., Struhsaker, T. T. 1978. Phenolic content of vegetation in two African rain forests: Ecological implications. *Science* 202:61–64

106. McNeil, M. 1964. Laterite soils. *Sci. Am.* 211:68–73

107. Medina, E. 1984. Nutrient balance and physiological processes at the leaf level. In *Physiological Ecology of Plants of the Wet Tropics*, ed. E. Medina, H. A. Mooney, C. Vázquez-Yanez, pp. 134–54. The Hague: Junk

108. Medina, E., Klinge, H. 1983. Productivity of tropical forests and tropical woodlands. In *Encyclopedia of Plant Physiology 12D: Ecosystem Processes: Mineral cycling, productivity, and man's influence*, ed. O. Lange, P. S. Nobel, C. B. Osmond, M. H. Ziegler, pp. 281–301. Berlin: Springer-Verlag

109. Melillo, J. M., Aber, J. D., Muratore, J. M. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–26

110. Mueller-Dombois, D., Vitousek, P. M., Bridges, K. W. 1984. *Canopy Dieback and Ecosystem Processes in Pacific Forests. Hawaii Bot. Sci. Pap. 44.* Manoa: Univ Hawaii. 100 p

111. Nadkarni, N. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* 16:249–56

112. Nátr, L. 1972. Influence of mineral nutrients on photosynthesis in higher plants. *Photosynthetica* 6:80–99

113. Nye, P. H. 1958. The relative importance of fallows and soils in storing plant nutrients in Ghana. *J. W. Afr. Sci. Assoc.* 4:31–50

114. Nye, P. H. 1961. Organic matter and nutrient cycles under moist tropical forest. *Plant Soil* 13:333–45

115. Nye, P. H., Greenland, D. J. 1960. *The Soil Under Shifting Cultivation. Tech. Commun. 51.* Farnham Royal, England: Commonwealth Bur. Soils, Commonwealth Agric. Bur.

116. Oates, J. F. 1978. Water-plant and soil consumption by Guereza monkeys *(Colobus guereza)*: A relationship with minerals and toxins in the diet? *Biotropica* 10:241–53

117. Ong, J. E., Gong, W. K., Wong, C. H.

118. Ovington, J. D., Olson, J. S. 1970. Biomass and chemical content of El Verde lower montane rain forest plants. In *A Tropical Rain Forest*, ed. H. T. Odum, R. F. Pigeon, pp. H53–77. Oak Ridge, Tenn: US Atomic Energy Comm.

119. Parker, G. G. 1983. Throughfall and stemflow in the forest nutrient cycle. *Adv. Ecol. Res.* 13:57–133

120. Parker, G. G. 1985. *The effect of disturbance on water and solute budgets of hillslope tropical rainforest in northeastern Costa Rica.* PhD thesis. Univ. Georgia, Athens. 161 pp.

121. Peace, W. J. H., Macdonald, F. D. 1981. An investigation of the leaf anatomy, foliar mineral levels, and water relations of trees of a Sarawak forest. *Biotropica* 13:100–109

122. Post, W. M., Emanuel, W. R., Zinke, P. J., Stangenberger, A. G. 1982. Soil carbon pools and world life zones. *Nature* 298:156–59

123. Proctor, J. 1984. Tropical forest litterfall. II. The data set. In *Tropical Rain forest: The Leeds Symposium*, ed. S. L. Sutton, A. C. Chadwick, pp. 83–113. Leeds: Leeds Philos. Nat. Hist. Soc.

124. Proctor, J. Nutrient cycling in primary and old secondary rain forests. *Advances in Physical Geography*. In press

125. Proctor, J., Anderson, J. M., Chai, P., Vallack, H. W. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure, and floristics. *J. Ecol.* 71:237–60

126. Richards, P. W. 1952. *The Tropical Rainforest.* Cambridge: Cambridge Univ. Press

127. Robertson, G. P. 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. *Oecologia* 61:91–104

128. Robertson, G. P., Herrera, R., Rosswall, T. H., eds. 1982. *Nitrogen Cycling in Ecosystems of Latin America and the Caribbean.* The Hague: Nijhoff/Junk 430 pp.

129. Robertson, G. P., Rosswall, T. 1986. Nitrogen in West Africa: The regional cycle. *Ecol. Monogr.* 56:43–72

130. Rodin, L. E., Bazilevich, N. I. 1967. *Production and Mineral Cycling in Terrestrial Vegetation.* Edinburgh: Oliver & Boyd

131. Russell, A. E., Ewel, J. J. 1985. Leaching from a tropical andept during big

storms: A comparison of three methods. *Soil Science* 139:181–89

132. Russell, C. E. 1983. *Nutrient cycling and productivity in native and plantation forests at Jarí Florestal, Pará, Brazil.* PhD thesis. University Ga., Athens

133. Salati, E., Sylvester-Bradley, R., Victoria, R. L. 1982. Regional gains and losses of nitrogen in the Amazon Basin. See Ref. 128, pp. 367–76

134. Salati, E., Vose, P. B. 1984. Amazon Basin: A system in equilibrium. *Science* 225:129–38

135. Sanchez, P. A. 1976. *Properties and Management of Soils in the Tropics.* New York: Wiley

136. Sanchez, P. A. 1981. Soils of the humid tropics. In *Blowing in the Wind: Deforestation and Long-range Implications,* ed. Department of Anthropology pp. 347–410. Williamsburg, Va: Col. William and Mary

137. Sanchez, P. A., Bandy, D. E., Villachica, J. H., Nicholaides, J. J. 1982. Amazon basin soils: Management for continuous crop production. *Science* 216: 821–27

138. Sanchez, P. A., Palm, C. A., Szott, L. T., Davey C. B. 1985. Tree crops as soil improvers in the humid tropics? *Attributes of Trees as Crop Plants,* ed. M. G. R. Cannell, J. E. Jackson. pp. 331–62. Huntingdon, UK: Inst. Terrestrial Ecol.

139. Sanford, R. L. Jr. 1985. *Root ecology of mature and successional Amazon forests.* PhD thesis. Univ. Calif., Berkeley

140. Sanford, R. L. Jr., Saldarriaga, J., Clark, K. E., Uhl, C., Herrera, R. 1985. Amazon rain-forest fires. *Science* 227:53–55

141. Servant, J., Delmas, R., Rancher, J., Rodriquez, M. 1984. Aspects of the cycle of inorganic nitrogen compounds in the tropical rain forest of the Ivory Coast. *J. Atmos. Chem.* 1:391–401

142. Sioli, H. (ed). 1984. *The Amazon: Limnology and Landscape Ecology of a Mighty Tropical River and its Basin.* Dordrecht: Junk

143. Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Can. J. Bot.* 50:2227–33

144. Sollins, P., Spycher, G., Glassman, C. A. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. *Soil Biol. Biochem.* 16:31–37

145. Sombroek, W. G. 1984. Soils of the Amazon region. See Ref. 142, pp. 521–35

146. Stark, N. 1971. Nutrient cycling. II.

Nutrient distribution in Amazonian vegetation. *Trop. Ecol.* 12:177–201

147. Stark, N., Jordan, C. F. 1978. Nutrient retention by the root mat of an Amazonian rain forest. *Ecology* 59:434–37

148. Stark, N., Spratt, M. 1977. Root biomass and nutrient storage in rainforest oxisols near San Carlos de Rio Negro. *Trop. Ecol.* 18:1–9

149. Steinhardt, V., Fassbender, H. W. 1979. Características y composición químicas de las lluvias de los Andes occidentales de Venezuela. *Turrialba* 29:175–82

150. St. John, T. V., Coleman, D. C. 1983. The role of mycorrhizae in plant ecology. *Can. J. Bot.* 61:1005–13

151. Sutton, S. L., Whitmore, T. C., Chadwick, A. C. (ed). 1983. *Tropical Rain Forest: Ecology and Management.* Oxford: Blackwell Sci. 498 pp

152. Sylvester-Bradley, R., de Oliveira, L. A., de Podesta Filho, J. A., St. John, T. V. 1980. Nodulation of legumes, nitrogenase activity of roots and occurrence of nitrogen fixing *Azospirillum* spp. in representative soils of Central Amazonia. *AgroEcosystems* 6:249–66

153. Tanner, E. V. J. 1977. Four montane rainforests of Jamaica: A quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J. Ecol.* 65:883–918

154. Tanner, E. V. J. 1981. The decomposition of leaf litter in Jamaican montane rain forests. *J. Ecol.* 69:263–73

155. Tanner, E. V. J. 1985. Jamaican montane forests: Nutrient capital and cost of growth. *J. Ecol.* 73:553–68

156. Tsutsumi, T., Nishitani, Y. 1984. On the effects of soil fertility on the throughfall chemicals in a forest. *Japan. J. Ecol.* 34:321–30

157. Turvey, N. D. 1974. Water in the nutrient cycle of a Papuan rain forest. *Nature* 251:414–15

158. Uehara, G., Gillman, G. 1981. *The Mineralogy, Chemistry, and Physics of Tropical Soils with Variable Charge Clays.* Boulder, Colo: Westview

159. United States Department of Agriculture. 1975. *Soil Taxonomy.* Soil Conserv. Serv. Agric. Handbk 436. Washington, DC: USGPO

160. Van Cleve, K., Oliver, L., Schlentner, R., Viereck, L. A., Dyrness, C. T. 1983. Productivity and nutrient cycling in taiga forest ecosystems. *Can. J. For. Res.* 13:747–67

161. Van den Driessche, R. 1974. Prediction

of mineral nutrient status of trees by foliar analysis. *Bot. Rev.* 40:347–94

162. Van Schaik, C. P., Mirmanto, E. 1985. Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica* 17:196–205

163. Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. *Am. Nat.* 119:553–72

164. Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–98

165. Vitousek, P. M., Denslow, J. S. 1987. Nitrogen and phosphorus availability in treefall gaps in a lowland tropical rainforest. *J. Ecol.* In press

166. Vitousek, P. M., Reiners, W. A. 1975. Ecosystem succession and nutrient retention: A hypothesis. *BioScience* 25:376–81

167. Vitousek, P. M., Van Cleve, K., Balakrishnan, N., Mueller-Dombois, D. 1983. Soil development and nitrogen turnover on recent volcanic substrates in Hawaii. *Biotropica* 15:268–74

168. Vogt, K. A., Grier, C. C., Meier, C. E., Keyes, M. R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabalis* stands in western Washington, as affected by fine-root input. *Ecol. Monogr.* 53:139–57

169. Walker, T. W., Syers, J. K. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19

170. Waring, R. H., Schlesinger, W. H. 1985. *Forest Ecosystems: Concepts and Management.* Orlando: Academic Press. 340 pp.

171. Waterman, P. G. 1983. Distribution of secondary metabolites in rain forest plants: Toward an understanding of cause and effect. See Ref. 151, pp. 167–79

172. Went, F. W., Stark, N. 1968. Mycorrhiza. *BioScience* 18:1035–39

173. Whitmore, T. C. 1975. *Tropical Rain Forest of the Far East.* London: Oxford Univ. Press

174. Whittaker, R. H. 1975. *Communities and Ecosystems.* New York: Macmillan

175. Whittaker, R. H., Likens, G. E. 1973. Carbon in the biota. In *Carbon and the Biosphere,* ed. G. M. Woodwell, E. V. Pecan. *Atomic Energy Comm. Symp. Ser. 30: CONF-720510.* Springfield, Va: Nat. Tech. Inf. Serv.

176. Zonn, S. V., Li, C.-K. 1962. Dynamics of the breakdown of litter, and seasonal changes in their ash composition, in two types of tropical biogeocoenoses. *Soobshcheniye Lab. Lesoved. Moskua* 6:144–52

Annual Review of Ecology and Systematics
Volume 17, 1986

CONTENTS

(continued)   vii

viii   CONTENTS   *(continued)*