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SECONDARY SUCCESSION FOLLOWING SLASH AND BURN AGRICULTURE IN NORTH-EASTERN INDIA

II. NUTRIENT CYCLING

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SUMMARY

(1) The accumulation of elements by vegetation and their rate of uptake and release through litterfall were determined in stands developed during 20 years after shifting agriculture. The concentrations of nitrogen, phosphorus and potassium were higher in the living aerial biomass than in the litter. Trees were found to have a high concentration of calcium, a bamboo of potassium, and herbaceous species of phosphorus.

(2) The elements in the above-ground living biomass increased linearly with increase in the age of the fallow until, in the 20-year old fallow, the densities were (g m^{-2}): 49, nitrogen; 6, phosphorus; 138, potassium; 44, calcium; and 23, magnesium. In fallows 10–20 years old, bamboo alone contained 40–45% of the nitrogen, 44–49% of the phosphorus, 54–60% of the potassium, 17–20% of the calcium and 35–40% of the magnesium in the total vegetation.

(3) The annual rate of accumulation was maximal after 15–20 years for nitrogen (2·5 g m^{-2} $year^{-1}$), 10–15 years for potassium (8·1 g m^{-2} $year^{-1}$), and during the first year for phosphorus (0·4 g m^{-2} $year^{-1}$). Potassium showed the highest rate of accumulation in different fallows and was 2·5- to 4·5-fold higher than calcium and 3- to 14-fold higher than magnesium.

(4) The enrichment quotient (the weight of an element in the vegetation divided by its rate of uptake) was higher for phosphorus and potassium than for nitrogen, calcium and magnesium, indicating the rapid rate of accumulation of phosphorus and potassium in the standing biomass. The density of elements in the soil was minimal in 5–10 year old fallows. The annual return of elements through litterfall increased with the age of the fallow during the 20 years of study.

INTRODUCTION

In slash and burn agriculture, a knowledge of the cycling of chemical elements is essential to understand the way in which the fertility, which is lost during the cropping period, is restored during the fallow period. Compared with temperate forests, relatively little is known about nutrient cycling in tropical and subtropical forests (Greenland & Kowal 1960; Nye 1961; Jordan & Kline 1972; Golley *et al.* 1975; Grubb & Edwards 1982). Nevertheless, these studies suggest certain patterns; the annual rate of uptake and return of elements may be greater in tropical forests than in temperate forests and a larger proportion of the elements appear to be in the vegetation (Rodin & Bazilevich 1967; Edwards & Grubb 1982).

The work of Bartholomew, Meyer & Laudelout (1953) is one of the few attempts to study the pattern of element cycling in tropical secondary successional fallows after slash and burn agriculture. They concluded that the storage capacity of leaves and litter is saturated at an early stage in the succession and, thereafter, the total storage capacity increases more slowly and in the woody material only. They found that the potassium accumulation was due to the dominance of *Musanga cecropioides* in the early stages. In the previous paper (Toky & Ramakrishnan 1983), the secondary succession and biomass and production patterns during the 20 years subsequent to slash and burn agriculture at low altitudes in the hill areas of Meghalaya in north-eastern India were described. The aim of this paper is to determine the patterns of elements accumulation in the vegetation and soil and the rate of transfer of the elements between the vegetation, litter and soil in these successions. The study was restricted to the aerial shoots and no measurements were made of throughfall.

METHODS

The study area was described in the previous paper (Toky & Ramakrishnan 1983).

Soil

The soil sampling from the three replicate sites of each age was carried out in March 1979 from depths of 0–7 cm, 7–14 cm, 14–28 cm and 28–40 cm. Ten samples were collected from each site at 20-m intervals along the transect (Ramakrishnan & Toky 1981; Toky & Ramakrishnan 1983) and a composite sample was prepared for each depth.

The soil was dried, ground and passed through a 2-mm sieve and analyses were made following the procedures given by Allen *et al.* (1974). Nitrogen was determined by the Kjehdahl method. Available phosphorus was measured colorimetrically by the ammonium-molybdate method after extraction with Bray & Kurtz's (1945) solution. Cations were extracted with 1 M ammonium acetate solution at pH 7. Calcium and magnesium were estimated by EDTA titration, and potassium by flame-emission.

The weight of each element (m^{-2}) was calculated to a depth of 40 cm using bulk density estimates of 1·4 for 0–14 cm and 1·5 for 14–40 cm depths. Bulk density or volume weight (the quotient of the dry weight of soil to the total volume it occupies in the field) was determined from the air-dry mass of a known field volume of soil. The soil was removed as a disturbed sample and the excavated hole was filled with a measured volume of sand (British Standards Institution 1967).

Aerial shoots and litter

The biomass of different fallows was determined during October–November 1979 for herbs, shrubs, bamboo, and trees. The samples from each predominant species were analysed separately, but all minor species (those with an importance value index less than 5) were combined into a composite sample. However, in both cases, leaves, branches, and boles were analysed separately. The litterfall was collected at monthly intervals from August 1978 to July 1979, and the litter on the ground was sampled in October–November 1979, and classified into leaves and twigs, and further subdivided into dicotyledons, bamboo, and other grass species. After similar separation into different categories according to species and litter types, the litterfall collected during the year was mixed into composite samples.

Plant and litter samples were ground to a powder and passed through a 0·5-mm sieve. Plant analyses were then made following the procedures given for soil except that the cation estimation was made after dry ashing and dissolving the ash in dilute HCl and, for estimation of total phosphorus, the samples were dry ashed with $MgNO_3$.

The total element density of each compartment was computed.

Total

The total quantities of elements in the ecosystem to a soil depth of 40 cm were calculated.

In the present study, only the soil and vegetation are considered. For each, the fractional annual turnover of each element was calculated by dividing the weight that left the compartment by the weight held in that compartment and expressed as a percentage (Reiners & Reiners 1970). Thus, for the vegetation, the weight lost through litterfall was divided by the weight in the vegetation and, for the soil, the weight taken up by the vegetation was divided by the weight in the soil. In order to compare the rates at which elements are incorporated into the vegetation, the enrichment quotient was calculated for each stand as the quotient of the weight of a given element in the vegetation divided by its rate of uptake by the vegetation (increase in the above-ground living biomass + annual litterfall) (Woodwell, Whittaker & Houghton 1975).

RESULTS

Aerial shoots

The leaves had the highest concentration of elements and the boles had the lowest (Fig. 1). The concentration of nitrogen, phosphorus and potassium was much higher in the branches and leaves than in the litter, but the concentration of calcium and magnesium was about the same in all three compartments. The concentration of calcium and magnesium in different compartments of the trees and shrubs was higher than in bamboo (*Dendrocalamus hamiltonii* Nees & Arn.) and herbaceous species but the bamboo had a significantly greater concentration of potassium than the other groups ($P < 0{\cdot}05$). The herbaceous species showed a markedly higher concentration of nitrogen and phosphorus than trees, shrubs and bamboo.

The density of elements in the aerial shoots increased with the age of the fallow during the 20 years studied (Table 1). Herbaceous species contained all the elements in the first year, 66% after 5 years, and a negligible amount in older fallows. The bamboo,

TABLE 1. Element density (g m^{-2}) in various compartments of living aerial shoot biomass during 20 years succession following slash and burn agriculture in Meghalaya, north-eastern India. $n = 15$.

Succession age (years)...		1	5	10	15	20
Trees and shrubs	N	—	2·6	11·0	18·5	29·2
	P	—	0·3	1·3	2·2	3·6
	K	—	5·6	21·8	38·7	62·5
	Ca	—	3·2	13·1	22·8	36·6
	Mg	—	1·3	5·5	9·3	14·8
Bamboo	N	—	0·6	8·2	15·3	19·6
	P	—	0·1	1·2	2·2	2·8
	K	—	2·3	32·4	58·9	75·4
	Ca	—	0·2	3·2	5·6	7·4
	Mg	—	0·2	3·3	6·1	7·8
Herbs	N	3·1	11·1	0·1	0·1	0·1
	P	0·5	1·6	0·02	0·01	0·01
	K	3·5	11·0	0·1	0·1	0·04
	Ca	1·4	4·5	0·1	0·02	0·02
	Mg	1·5	5·0	0·1	0·03	0·02

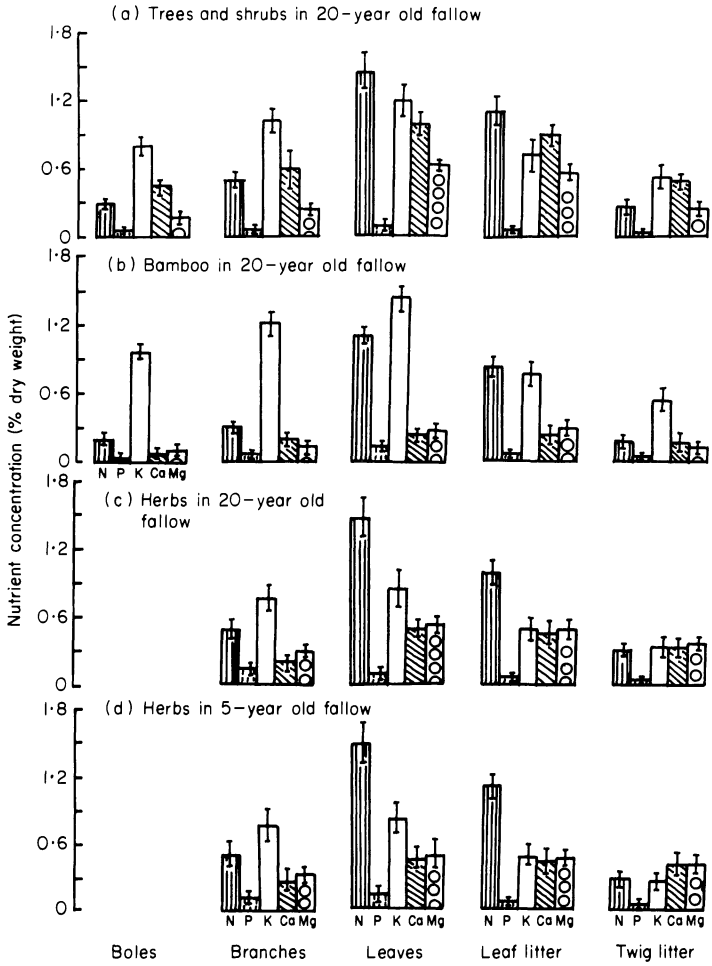

FIG. 1. Element concentration (% dry weight) in boles, branches, leaves, leaf litter, and twig litter in a 20-year old fallow: (a), trees and shrubs; (b), bamboo; (c), herbs; and (d), herbs in a 5-year old fallow, in Meghalaya, north-eastern India. $n = 15$. Vertical bars represent 1 S.E.M.

Dendrocalamus hamiltonii, contained 40–45% of the nitrogen, 44–49% of the phosphorus, 54–60% of the potassium, 17–20% of the calcium and of the 35–40% magnesium in the aerial shoots of the 10–20 year old fallows. The amounts in trees and shrubs increased between years 5 and 20, with proportionally more calcium to potassium than bamboo.

Figure 2 shows the pattern of distribution of the elements in the boles, branches and leaves of all the plants. The boles had greatest amounts and the leaves least in the fallows of 10–20 years of age. In the 1-year old fallow, which was devoid of trees, the stem and branches contained much of the elements, whereas leaves had a greater proportion of the elements in 1- and 5-year old fallows than in the older fallows. Potassium, calcium, magnesium and phosphorus were mainly in the bole and branches whereas the proportion of nitrogen was greatest in the leaves.

The rate of accumulation of nitrogen, phosphorus and magnesium decreased during the first 10 years and then increased sharply during the next 10 years, whereas calcium

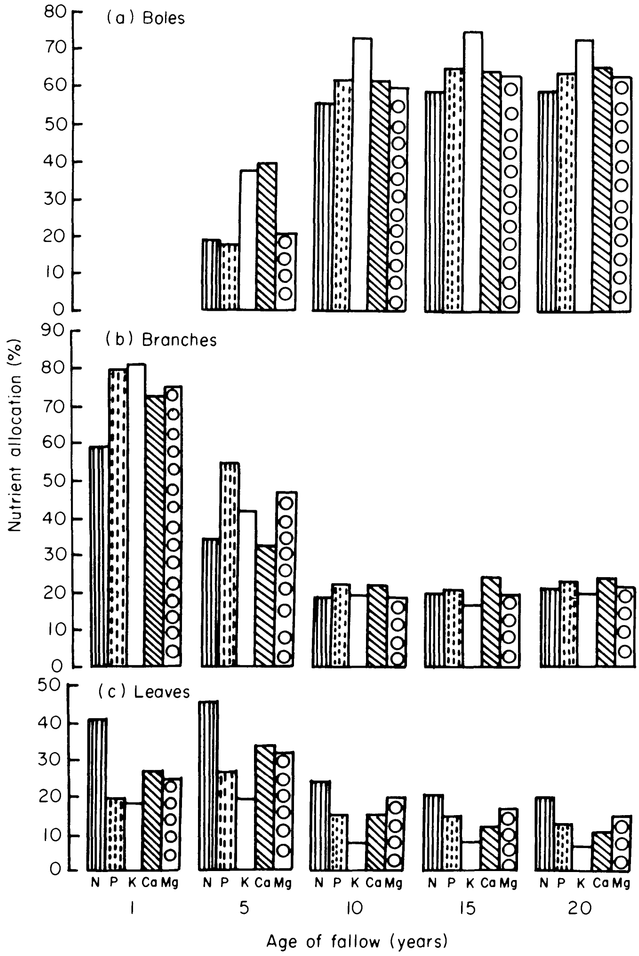

FIG. 2. Percentage distribution of elements in the above-ground vegetation in successional communities up to 20 years old in Meghalaya, north-eastern India: (a), boles; (b), branches; and (c), leaves.

TABLE 2. Rates of accumulation of elements (g m^{-2} $year^{-1}$) in the living aerial shoot biomass during twenty years succession following slash and burn agriculture in Meghalaya, north-eastern India.

Age of fallow (years)	N	P	K	Ca	Mg
0–1	1·8	0·4	2·7	0·6	0·9
1–5	1·5	0·3	3·0	1·2	0·9
5–10	1·4	0·1	6·9	1·6	0·5
10–15	2·4	0·3	8·1	2·2	1·2
15–20	2·5	0·4	7·6	2·8	1·2

showed a steady increase during the 20 years and potassium increased for 15 years and then decreased (Table 2).

Table 3 presents the annual rate of uptake of each element into the aerial shoot and their enrichment quotients. The rate of uptake of all the elements increased during the 20 years.

TABLE 3. Rates of uptake of elements (g m^{-2} $year^{-1}$) in the living aerial shoot biomass (including the annual litterfall) during 20 years succession following slash and burn agriculture in Meghalaya, north-eastern India. Values in parentheses are the enrichment quotients (element held in vegetation/element uptake) of Woodwell, Whittaker & Houghton 1975).

Years	N	P	K	Ca	Mg
0–1	3·1	0·5	3·5	1·5	1·5
	(0·9)	(1·0)	(0·9)	(0·9)	(1·0)
1–5	5·7	0·5	6·0	4·3	3·0
	(2·5)	(4·0)	(3·0)	(1·8)	(2·1)
5–10	7·6	0·4	12·0	5·3	3·1
	(2·5)	(6·2)	(4·5)	(3·1)	(2·8)
10–15	9·2	0·7	13·5	6·3	4·2
	(3·7)	(6·3)	(7·2)	(4·5)	(3·7)
15–20	10·9	0·9	14·5	7·8	4·8
	(4·5)	(7·1)	(9·5)	(5·6)	(4·7)

Potassium was accumulated in the largest quantity, followed by nitrogen and calcium; phosphorus showed the least uptake. The enrichment quotient for each element increased in a similar manner. The quotient was much higher for potassium and phosphorus than for the other elements studied.

Soil

The total density of nitrogen in the soil (to a depth of 40 cm) increased for the first 10 years and then stabilized at a slightly lower level, whereas the available phosphorus increased during the 20 years (Table 4). Exchangeable potassium, calcium and magnesium started with high densities (after burning), declined for a few years and then increased; potassium showed the greatest change.

TABLE 4. Density of elements (g m^{-2}) in living aerial shoots, soil, and litter on the ground during 20 years succession following slash and burn agriculture in Meghalaya, north-eastern India.

Succession age (years)...		1	5	10	15	20
Living aerial shoots	N	3	14	19	34	49
	P	1	2	3	4	6
	K	4	19	54	98	138
	Ca	1	8	16	28	44
	Mg	2	7	9	15	23
Soil (0–40 cm)	N	978	1110	1225	1055	1050
	P	1	1	2	2	3
	K	99	57	26	118	120
	Ca	136	80	104	109	108
	Mg	130	108	72	120	121
Litter on ground	N	0·3	0·8	1·8	2·3	2·1
	P	0·01	0·05	0·1	0·1	0·1
	K	0·1	0·1	0·5	0·3	0·7
	Ca	0·2	0·5	1·1	0·8	1·4
	Mg	0·1	0·4	0·9	0·6	0·8
Total ecosystem	N	981	1125	1246	1091	1101
	P	2	3	5	6	9
	K	103	76	81	216	259
	Ca	138	88	121	138	153
	Mg	132	115	82	136	144

Total

The density of nitrogen in the whole ecosystem was highest in the 10-year old fallow, whereas the density of phosphorus increased throughout (Table 4). Initially, the density of cations was high (after the burn); it declined to a minimum after 5–10 years, but it increased subsequently to a maximum in the 20-year old fallow. The proportion of different elements in the living biomass (compared to the soil) gradually increased with age especially for phosphorus and potassium.

Litterfall

The annual rate of return of elements through the litterfall increased with the age of the fallow (Table 5). The return of nitrogen was greatest, followed by potassium and calcium. In the 1-year fallow, elements were returned exclusively through leaf litter and, in the 5-year old fallow, the contribution by twigs of dicotyledons was at a maximum (18% of the total). In the 20-year old fallow, 94% of the elements in the litterfall were in the leaves. In general, the nitrogen accumulation by bamboo was much less than other species and, in older fallows, where bamboo was a major component, its accumulation of potassium and phosphorus equalled or exceeded that of the other species combined; its accumulation of magnesium was relatively low.

The quotient of the annual return of elements through litterfall to the annual uptake by the vegetation, expressed as a percentage, increased for 5 years for potassium and for 10 years for other elements; later, it tended to stabilize at a slightly lower level (Fig. 3). The retention of potassium in the living biomass was high as the proportion returned through

TABLE 5. Density of elements in various components of litterfall (g m^{-2} $year^{-1}$) during 20 years succession following slash and burn agriculture in Meghalaya, north-eastern India.

Succession age (years)...		1	5	10	15	20
Leaves (excluding bamboo)	N	1·3	3·7	3·4	3·9	4·6
	P	0·1	0·2	0·1	0·2	0·2
	K	0·8	2·1	2·2	2·6	3·0
	Ca	0·9	2·4	2·7	3·1	3·7
	Mg	0·6	1·7	1·6	1·9	2·2
Bamboo leaves	N	0	0·1	2·6	2·7	3·5
	P	0	0·01	0·2	0·2	0·3
	K	0	0·1	2·4	2·4	3·2
	Ca	0	0·03	0·7	0·7	1·0
	Mg	0	0·03	0·9	0·9	1·2
Twigs (excluding bamboo)	N	0	0·4	0·1	0·1	0·1
	P	0	0·04	0·02	0·01	0·01
	K	0	0·8	0·3	0·1	0·2
	Ca	0	0·7	0·2	0·1	0·2
	Mg	0	0·4	0·1	0·1	0·1
Bamboo twigs	N	0	0	0·1	0·1	0·2
	P	0	0	0·01	0·02	0·02
	K	0	0	0·2	0·3	0·5
	Ca	0	0	0·1	0·1	0·1
	Mg	0	0	0·04	0·1	0·1
Total	N	1·3	4·2	6·2	6·8	8·4
	P	0·1	0·2	0·3	0·4	0·5
	K	0·8	3·0	5·1	5·4	6·9
	Ca	0·9	3·1	3·7	4·1	5·0
	Mg	0·6	2·1	3·6	3·0	3·6

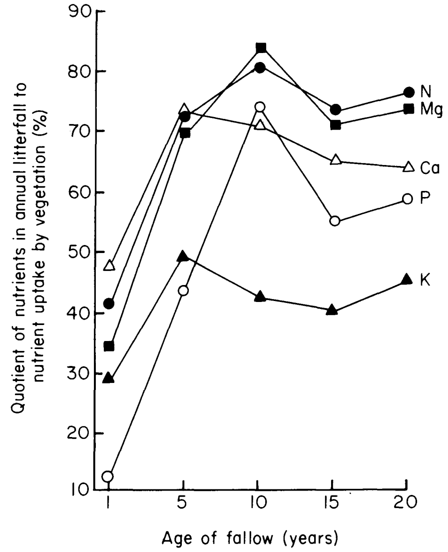

FIG. 3. The quotients of the annual return of elements through litterfall to the annual uptake by the vegetation, expressed as percentage, in successional communities up to 20 years old in Meghalaya, north-eastern India. Symbols: ●, N; ○, P; ▲, K; △, Ca; ■, Mg.

the litterfall was low; that of phosphorus was almost as high, whereas the retention of nitrogen was the lowest of all the elements studied.

Element turnover

The annual turnover of the different elements for the soil and vegetation is given in Table 6. Those for nitrogen, calcium and magnesium in the soil increased with the age of the fallow, while those for phosphorus and potassium were maximal at 5 and 10 years, respectively. The annual turnover of all elements in the vegetation followed a consistent pattern of decrease with age. The percentage turnover of phosphorus and potassium was generally higher in the soil than in the vegetation.

TABLE 6. The fractional annual turnover of elements (the weight that left the compartment divided by the weight held in that compartment, expressed as percentage) (Reiners & Reiners 1970) of soil and vegetation during 20 years succession following slash and burn agriculture in Meghalaya, north-eastern India.

Fallow age (years)	N		P		K		Ca		Mg	
	Soil	Vegetation	Soil	Vegetation	Soil	Vegetation	Soil	Vegetation	Soil	Vegetation
1	0·3	42	50	10	3	20	1	64	1	40
5	0·5	29	50	11	10	16	5	39	3	32
10	0·6	32	20	12	46	9	5	23	4	29
15	0·8	20	35	10	11	6	6	15	3	20
20	1·0	17	30	8	12	5	7	11	4	16

DISCUSSION

In this comparative study of the element concentration in the different compartments of the vegetation during a 20 year fallow, the concentration in the litter was, in general, lower than that in the living biomass. This may partly be due to translocation before abscission (Kramer & Kozlowski 1960). The withdrawal of appreciable quantities of nitrogen before abscission has been suggested by Grubb & Edwards (1982) also. In addition, some of the elements may be leached into throughfall before litterfall occurs. It may be noted that potassium, which is more readily leachable (Nye & Greenland 1960), had a much lower concentration in the litter than in the living biomass.

Among the cations in the living biomass, the concentration of potassium was much higher in the 20-year old fallow than in the younger fallows, especially in the bamboo, *Dendrocalamus hamiltonii*. The higher concentration of potassium in bamboo is due to its fast accumulation by this species which is an important component of the early secondary succession. This is obvious when the total density of potassium in the living biomass of the bamboo in a 15–20-year fallow is compared with that held in all the other species of trees and shrubs combined. Thus, in early succession studied here, potassium is predominant over calcium in the living biomass whereas other workers (Golley *et al.* 1975; Grubb & Edwards 1982) have shown a reverse trend in mature communities.

With the development of secondary vegetation, the weight of elements in the living biomass increased due to a linear increase in biomass with age (Toky & Ramakrishnan 1983). The high enrichment quotient (concentration in vegetation/uptake) for potassium in fallows 10–20 years old indicates a maximum accumulation of this element in the living biomass. A similar observation was made in early succession in Zaïre where *Musanga cecropiodes* selectively accumulated potassium (Bartholomew, Meyer & Laudelout 1953), though the quantities of potassium were much lower than in a 20-year fallow in the present study. It may be noted that, in north-eastern India, during the first 10 years of the fallow period, when bamboo is not a major component of the vegetation, the enrichment quotient for phosphorus was more than that for other elements indicating the selective accumulation of this element. For calcium and magnesium, the annual uptakes and enrichment quotients were much higher in older fallows, probably because of a rapid growth of trees. Greenland & Kowal (1960) reported almost three times more calcium than potassium in the above-ground biomass in a 40-year old forest in Ghana. Recent studies of Grubb & Edwards (1982) showed higher concentrations of calcium and magnesium than potassium in the trunks of large trees. The percentage of elements in the plant compartment of the aerial shoots for the 20-year old fallow is: N, 5%; P, 69%; K, 53%; Ca, 28%; Mg, 16%. A comparison of these results with those on the different rain forest types discussed by Edwards & Grubb (1982) suggests that, in contrast to the conventional idea of a tropical rain forest with about 90% of the element capital in the plants, the fraction in the present case is low.

The concentration of all the elements, except nitrogen, was generally higher in the soil under a 1-year old fallow that it was later; this followed their release due to the slash and burn (Table 4). The rapid decline in element concentration in the soil during the first 5–10 years is due to depletion by the rapidly developing vegetation. The return of elements to the soil starts after 10 years, after which there is a gradual increase in their density. For nitrogen, on the other hand, not only is it lost due to the fire, but its fixation may be adversely affected by the fire. However, soon after the fire, microbial activity increases rapidly, due partly to micro-environmental changes in the soil (Ahlgren & Ahlgren 1965) and also to the removal of allelopathic effects (Smith, Bormann & Likens 1968; Rice 1974), so that the increase in nitrogen density continues for 10 years; this is followed by a decline probably due to the establishment of a balance between nitrogen fixation and mineralization. Similar observations have been made for the 'Lua' forest fallow system of shifting agriculture in Thailand (Zinke, Sabhasri & Kunstadter 1978) and in south-western Nigeria (Aweto 1981).

The return of elements to the soil through litterfall increased with the age of the fallow; this is a function of the linear increase in the litterfall with age (Toky & Ramakrishnan 1983). A higher weight of potassium and lower weights of other elements are returned annually compared with the values reported by Ewel (1976) for fallows up to 14-years old in Guatemala. This is due to the relatively high concentration of potassium in the predominantly bamboo litter in Meghalaya, as already discussed.

While the annual percentage turnover of all elements in the soil tended to increase with fallow age, those of the vegetation decreased. This is to be expected because of the marked increase in uptake by the developing vegetation and increased storage in the living plants which is proportionately higher than the rate of release through litter. The only exceptions to this are for phosphorus and potassium which reached their maximum annual turnover in the soil in the 5–10-year old fallow. The high fractional turnover value for phosphorus in the soil in the 5-year old fallow may be due to a higher uptake by the herbaceous vegetation that predominates then, and that for potassium in the 10-year old fallow may be related to rapid growth of bamboo at this time.

Element cycling varies according to the supply from the soil. For example, in certain Amazonian forests (Klinge & Rodrigues 1968a, b; Stark 1971a, b) the podzols contain low element concentrations. As a consequence, the concentrations of elements in plants are much greater than in the soil and the elements released from the litter are rapidly taken up by the vegetation. This has led Stark (1971a) to propose the direct transport of elements from the dead organic matter to the living roots by mycorrhiza. In such a case, cutting and burning destroy the mycorrhizal connection and the recovery of the system may take a much longer time compared to other systems. There are abundant mycorrhiza on our study area too (H. K. Deka, unpublished).

After the destruction of element cycling by slash and burn agriculture, the system recovers rapidly through a quick succession and potassium, which is one of the important elements and highly susceptible to leaching and runoff losses during cropping and the early phases of regrowth (Toky & Ramakrishnan 1981), is rapidly conserved in the living biomass. As this process progresses steadily during the first 20 years or more, any disturbance—such as in the short agricultural cycle of 4–5 years, as is now common (Ramakrishnan *et al.* 1981)—is likely to adversely affect the recovery of soil fertility (Ramakrishnan & Toky 1981) and the element conservation by the system as a whole.

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