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The Journal of Ecology, Vol. 64, No. 1. (Mar., 1976), pp. 293-308.

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LITTER FALL AND LEAF DECOMPOSITION IN A TROPICAL FOREST SUCCESSION IN EASTERN GUATEMALA

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INTRODUCTION

Sixteen years ago, Nye & Greenland (1960), in referring to the humid tropics, noted that 'after a quarter of a century of experiment . . . we have failed to introduce . . . any method of staple food production superior to the system of natural fallowing used in shifting cultivation'. This statement is still valid. The key to the long-term success of shifting cultivation is the fallow period, when the complex of physical and chemical factors referred to as 'fertility' is restored to the site. If the fallow period is too short, site degradation takes place and yields decline; if it is too long, the system becomes impractical due to the vast amount of land required.

One of the most important functions of a fallow period is the accumulation of mineral nutrients and organic matter by native second-growth vegetation, a process which has been studied in various areas where shifting cultivation is practised, e.g. in Thailand (Zinke, Sabhasri & Kunstadter 1970), in various parts of Africa (Bartholomew, Meyer & Laudelot 1953; Laudelot & Meyer 1954; Greenland & Kowal 1960; Nye & Greenland 1960), and in tropical America (Snedaker 1970; Ewel 1971; Tergas & Popenoe 1971; Harcombe 1973). It is the return of the accumulated organic matter and nutrients to the upper soil layers which accounts for a large part of the restoration of fertility, and the main pathway for this return is the fall and subsequent decomposition of litter. The litter on the soil surface acts as an input-output system, receiving inputs from the vegetation and, in turn, decomposing and thereby supplying materials to the soil and roots. Litter accumulates on the soil until litter fall equals litter decomposition, after which the amount of litter accumulated on the soil surface oscillates around some mean steady-state value. The dynamics of this accumulation process are of particular interest in the lowland humid tropics, where rates of litter production and decomposition are high.

This study was designed to investigate litter in successional tropical vegetation, with special emphasis placed on determining the effects of age of vegetation, species and soil type on leaf decomposition. The study was carried out in the humid lowlands of eastern Guatemala, where shifting cultivation is the primary means of subsistence for a rapidly growing population of Kekchi Amerindians, who are migrating into the area from the overpopulated highlands. Their agricultural practices have been described by Carter (1969).

THE STUDY AREA

Field studies were conducted at Murcielagos Farm, on the north shore of Lake Izabal, almost midway between the towns of San Felipe and El Estor (Latitude 15°30'N,

Longitude 89°10'W) at an altitude of 10–100 m. There is a flat plain consisting of alluvial and lacustrine sediments extending c. 1–2 km north from the lake shore, a band of limestone foothills, with serpentine outcrops near their summits and a major east–west mountain range (primarily serpentine) along the north shore of the lake. The alluvial soils are partially inundated during each rainy season. Most of the shifting agriculture is concentrated on the alluvium and the limestone portions of the foothills, although plots are occasionally established on serpentine soils. Total annual rainfall at Murcielagos Farm is c. 2000 mm, about three-quarters of which falls between May and November.

Successional broad-leaved forests occupy most of the land on Murcielagos Farm, including some sites on serpentine, but pine savannas are common in the area on the poorest soils. The forest on the seasonally flooded soils of the flat plain contains more palms (chiefly *Astrocaryum mexicanum* Liebm. and *Orbignya cohune* Dahl ex Stand.) and is less completely deciduous than the forest on the slopes. The dominant trees attain heights of 30 to 35 m, those on the alluvium usually being somewhat taller than those on the slopes.

Most of the vegetation on the farm is in secondary succession and most stands are less than fifteen years old. When a cultivated field is abandoned, the site is rapidly covered with a mixture of herbaceous weeds, vines and woody coppice. After one year this vegetation is c. 2 m high (with some of the woody species emerging to 4 m) and it forms an almost impenetrable tangle. After three to four years most of the herbaceous plants are replaced by woody species, but the vines move up with the canopy. A secondary growth eight to ten years old is already a forest, with the canopy reaching a height of c. 10 m; the stand is open enough for one to move relatively freely within it. At twelve to fourteen years the canopy begins to stratify, with an upper story of pioneer emergents 15–20 m tall, e.g. *Ochroma lagopus* Sw. and *Cecropia peltata* L., and a lower-level canopy at about 8–12 m with more shade-tolerant species.

Stands of the following ages were selected for study: 1, 3, 4, 5, 6, 9 and 14 years. Two sites in what is referred to as 'mature forest' were included in this study for comparison with the young secondary stands: one on the alluvial soil and one on the limestone–serpentine foothills. The presence of some shade-intolerant species, such as *Bursera simaruba* (L.) Sarg. and *Pithecolobium saman* (Jacq.) Benth., suggests that these forests may be of secondary origin, but their exact age is unknown. The presence of epiphytes, shade-tolerant palms, large heavy fruits and a wide range of tree diameters indicates, however, that these forests are very close to the steady-state or climax condition.

METHODS

Field techniques

Litter production was measured in single stands of eight ages: 1, 3, 4, 5, 6, 9 and 14 years plus mature forest. All the sites were located on alluvial soils, between the lake shore and the foothills. Square collecting baskets of 0.8 m² internal surface area were used to intercept litter fall; larger collectors in the dense second-growth would have required excessive disturbance of the vegetation. The bottoms of the baskets were 1.6 mm mesh plastic screen. The baskets were placed flat on the soil surface, not elevated by legs; litter traps are usually raised to avoid excessive decomposition of the litter between harvests, but young second-growth vegetation produces leaves right down to ground level.

Twenty baskets were placed in each of the eight stands at 10-m intervals around the perimeter of a rectangular plot 90 × 10 m. All baskets were at least 30 m inside the stand.

They were placed in the field on 20 June 1966 and three collections were made between then and 25 August 1966. Fallen litter was harvested again on 24 December 1966 and on 20 June 1967.

Decomposition of leaves was investigated in stands of 0, 3, 6, 9 and 14 years of age, and in mature forest. Each of the six ages of vegetation was represented on the upland soils and the alluvial soils, for a total of twelve stands. Fallows of 0 years age were obtained by clearing 0.25 ha of young second-growth on both upland and lowland soils; these two sites were kept cleared of regrowth throughout the course of the study.

The five species listed below, all of which are common constituents of the second-growth stands in the area, were selected for the decomposition study with the aim of including as wide a range of leaf sizes, shapes and textures as possible.

(i) *Heliconia latispatha* Benth. (Musaceae) has leaves very similar to those of a banana. Only the leaf blades, including the prominent midrib, were used in the study; these average c. 1 × 0.3 m, and their moisture content is high (often >90% in fresh material). *Heliconia* often forms pure stands in the fallow, especially on poorly drained sites.

(ii) *Trema micrantha* Blume (Ulmaceae) has leaves similar in size and shape to those of *Ulmus* of Temperate Zone forests; the blade is 5–9 cm long, 2–4 cm wide. The petiole is c. 2 mm long and was left intact in this study. *Trema* is a common pioneer tree throughout most of the humid American tropics and attains a height of over 15 m.

(iii) *Cochlospermum vitifolium* Spreng. (Cochlospermaceae) has very soft orbicular palmatifid leaves with five pronounced lobes; they are 10–15 cm in diameter overall. The coarse, stiff petiole (c. 10 cm long and 2 mm thick) was included in this study. *Cochlospermum*, like *Trema*, is a common pioneer tree. It is usually found on the better-drained sites and, when mature, is c. 8 m tall.

(iv) *Paspalum fasciculatum* Willd. ex Fluegge (Gramineae) is a coarse bunch-grass, which grows about 1 m high and is particularly prevalent in areas where the soil has been disturbed, either by cultivation or by periodic fire. In second-growth vegetation it is usually found on those sites which are under a fallow-cultivation cycle of less than five years. In areas where the soil is cultivated mechanically it often forms continuous pure stands, completely dominating the site. The *Paspalum* used in the decomposition study was harvested from an oil palm plantation which had been cultivated and fertilized the year before. All of the above-ground parts of *Paspalum* were utilized.

(v) *Orbignya cohune* (Arecaceae) is a large palm with pinnately compound leaves, which are often more than 10 m long. Only the leaflets (50–80 cm long, 4 cm wide) were used in the decomposition study; they are very coarse-textured. *Orbignya* is found in the mature forests as well as in second-growth vegetation. When a field is cleared for planting the large palms are not usually cut down because the trunks are extremely hard; instead, the leaves are generally cut off, but when the field is abandoned new leaves sprout. Burning does not usually kill the palm. Fronds of *Orbignya* are extremely durable if kept off the soil and are used more commonly than those of any other palm for roof thatch in the Lake Izabal region.

Ideally, in a field study of decomposition, the samples should be kept free of contamination by other organic matter without retarding normal decomposition processes. Bags measuring 45 cm long by 25 cm wide were constructed for this purpose from plastic screening with a 1.6 mm mesh. The bags were stapled along the sides and the top at 5-cm intervals which left gaps large enough so that most arthropods could enter freely, yet the plant material was still retained. The use of bags containing homogeneous plant material in decomposition studies has been criticized by Wiegert & Evans (1964) and Wiegert &

Murphy (1968); Witkamp & Olson (1963) concluded that the use of bags resulted in slight underestimation of decomposition rates. In the present study, however, it was noted that within two weeks after placement in the field the litter bags were well incorporated into the natural litter and showed considerable evidence of decomposer activity.

Fresh plant material was gathered and placed in decomposition bags on 8 June 1966, after which the bags were hung under a thatch roof and air-dried until 14 June, when the weight of each bag of plant material (c. 200 g) was recorded to the nearest 0.05 g. Of the seventy-five bags of each of the five species, three were selected at random for subsequent determination of initial percentage dry weight and mineral nutrient content. The remainder were assigned at random to locations within each of the twelve stands; six bags of each species were placed in each stand.

A grid consisting of eleven parallel lines, 10 m apart, was laid out over 1 ha near the centre of each stand. Each interval of 1 m along these lines was considered to represent a sample location, with bags assigned at random to these points. An exception to this placement procedure was made in the more homogeneous cleared areas (0 yr plots), where all bags were assigned to random points within the central 0.1 ha of the plot.

Each bag was placed so that the lower surface was in contact with the soil and the upper surface was approximately level with the surrounding natural litter; it was then anchored in position with heavy gauge wire, which was hooked through one corner of the bag and driven into the soil.

The bags were collected after decomposition had proceeded for three periods of time: six, ten and twenty-seven weeks. At each collection-time, two randomly chosen bags of each species were recovered from each of the twelve sites.

Sample processing

All samples were collected in cotton bags and dried in a field oven at 45–55° C to retard decomposition, then shipped to Florida, where dry weights were obtained after drying for 24 h at 70° C, and were recorded to 0.1 g. Variation in percentage dry weight among the control bags did not exceed 4% for any of the five species.

All of the decomposition samples and the litter fall samples for the period 4 August–25 August were analysed for nitrogen, phosphorus, potassium, calcium and magnesium. The twenty samples of fresh litter from each stand were randomly pooled into five composites of four samples each. All samples were ground in a Wiley Mill to pass a no. 20 mesh screen. Each sample was thoroughly mixed before the 2.000-g subsample for analysis was extracted. Nitrogen was determined by the Kjeldahl method. Extracts for the determination of phosphorus and cations were prepared by ashing for 6 h at 500° C, adding an excess of 25% nitric acid, evaporating the acid, re-ashing as above, adding an excess of concentrated hydrochloric acid and evaporating it to dryness, taking up the ash in 10 N hydrochloric acid, filtering through number 42 Whatman filter paper, and making up to volume to yield a 0.1 N hydrochloric acid solution. Phosphorus was determined by the method of Truog (1930). Potassium was determined by emission flame photometry and calcium and magnesium were determined by atomic absorption flame photometry.

RESULTS

Litter production

The relationship between age of vegetation and litter production is shown in Fig. 1. The second-order polynomial used to draw the curve ($y = 5.698 + 0.643x - 0.05x^2$),

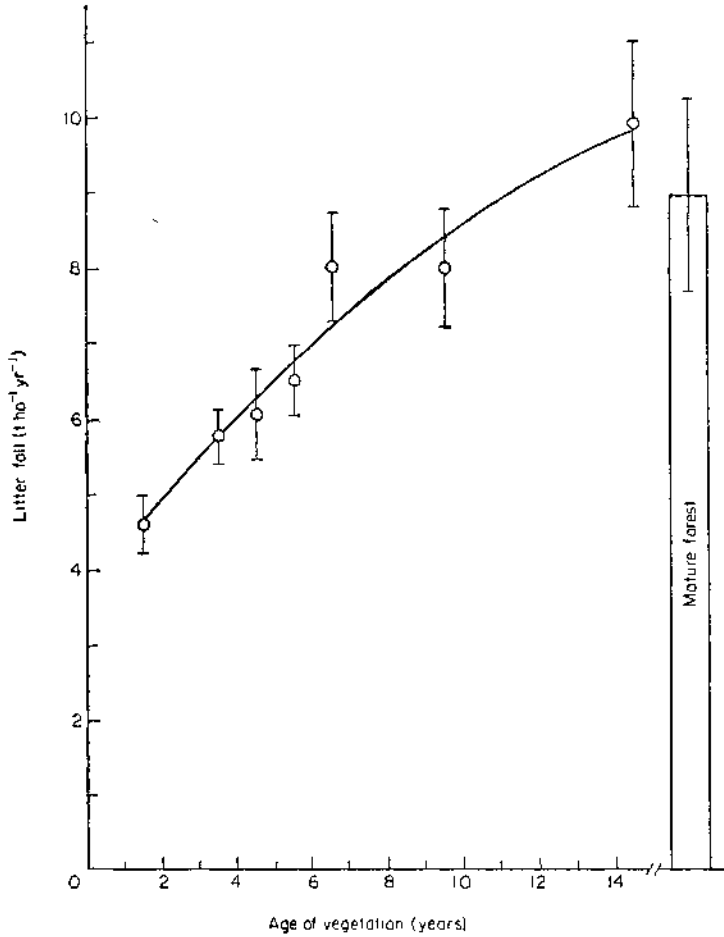


FIG. 1. Litter production as a function of the age of the vegetation. The column represents litter production in mature forest. Vertical bars indicate standard errors of the means.

Table 1. The mineral nutrient contents of freshly fallen litter (mean percentage dry weight \pm S.E.M.)

Age of vegetation (years)	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
1	1.61 \pm 0.28	0.070 \pm 0.015	0.228 \pm 0.064	1.54 \pm 0.19	0.87 \pm 0.13
3	1.68 \pm 0.24	0.064 \pm 0.014	0.286 \pm 0.126	1.40 \pm 0.27	0.91 \pm 0.20
4	1.69 \pm 0.14	0.067 \pm 0.002	0.186 \pm 0.042	0.66 \pm 0.17	0.82 \pm 0.22
5	1.36 \pm 0.18	0.046 \pm 0.007	0.185 \pm 0.075	0.86 \pm 0.26	0.84 \pm 0.04
6	1.77 \pm 0.30	0.074 \pm 0.016	0.254 \pm 0.090	1.88 \pm 0.68	0.44 \pm 0.18
9	1.80 \pm 0.11	0.060 \pm 0.006	0.153 \pm 0.018	0.68 \pm 0.35	1.18 \pm 0.30
14	1.45 \pm 0.15	0.066 \pm 0.005	0.242 \pm 0.049	2.13 \pm 0.37	0.36 \pm 0.06
Mature forest	1.88 \pm 0.53	0.064 \pm 0.016	0.220 \pm 0.069	0.98 \pm 0.11	0.71 \pm 0.26

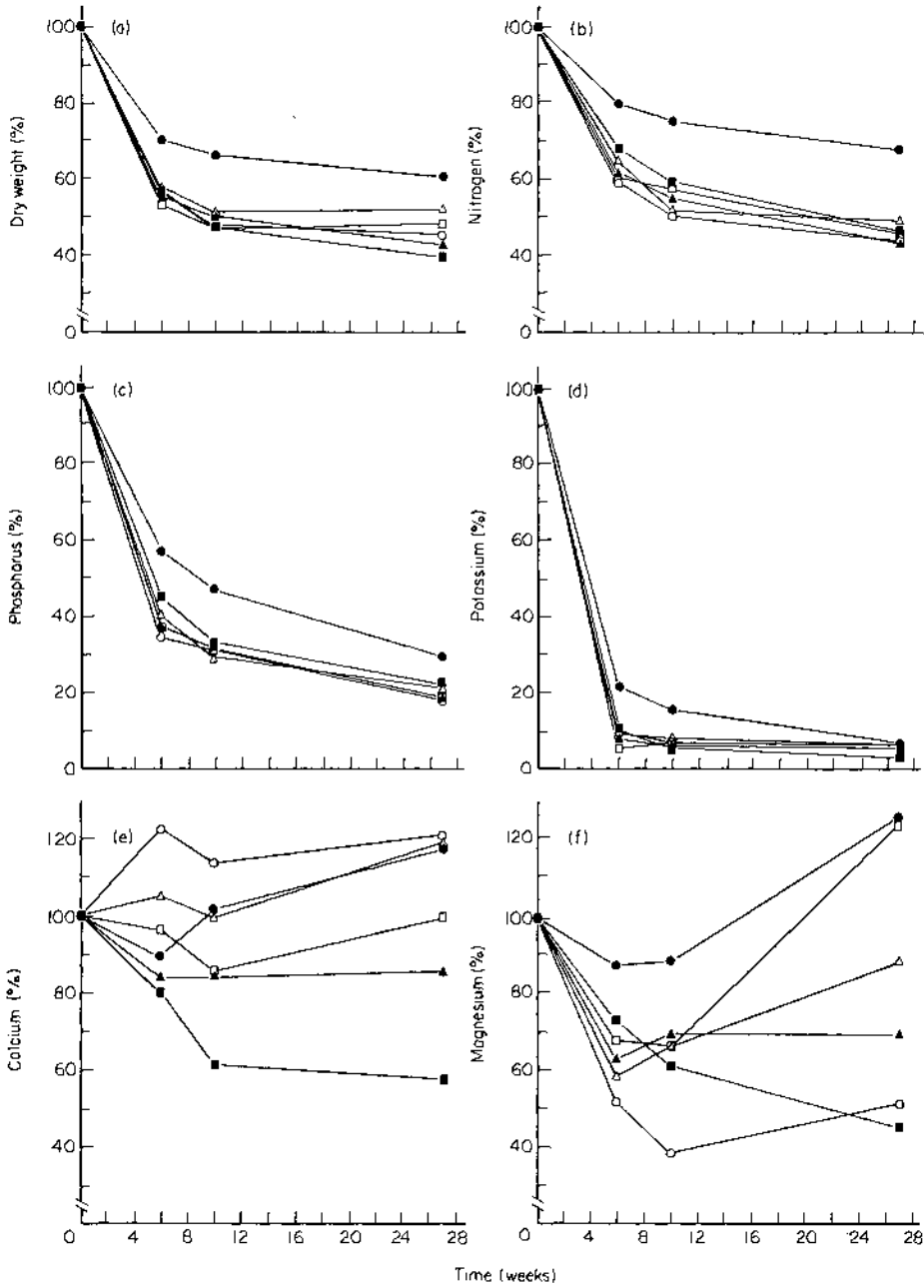


FIG. 2. Losses during decomposition under six ages of vegetation: 0 (●), 3 (□), 6 (■), 9 (△) and 14 (○) years, and mature forest (▲). Each point represents a mean of twenty values: two samples of five species from two soils. The values plotted are the percentages of the amount present at t_0 ; the mean concentrations at t_0 (% dry weight) were as follows: 1.93% N, 0.18% P, 1.41% K, 0.57% Ca and 0.62% Mg.

where y = litter production in metric tons per hectare per year and x = age of vegetation in years, was fitted by least-squares regression. The amounts of litter production shown must necessarily underestimate the actual amounts of litter fall because of decomposition which occurred during the long intervals between the third and fourth, and fourth and fifth collections. The values shown, therefore, are more valuable as indicators of differences in the amount of litter produced by different ages of vegetation than as measures of the absolute amount of litter produced in one year by each of the stands.

The nutrient content of the litter which fell between 4 August and 25 August is summarized in Table 1. There were few significant differences between sites for nitrogen, phosphorus and potassium, but calcium and magnesium contents were more variable.

Decomposition

The results of the leaf decomposition study were subjected to factorial analysis of variance, and significant differences ($P < 0.05$) were identified using Duncan's New Multiple Range Test (Steel & Torrie 1960). The results are described for each of the three main-effect treatments: age of vegetation, species subjected to decomposition and soil-type.

Effects of age of vegetation

In Fig. 2 data from samples of all five species and both soil-types are pooled for each of the six ages of vegetation. Loss of dry weight (Fig. 2(a)) occurred at much the same rate on all ten vegetated sites, but was 10–18% slower in the cleared areas. Decomposition was rapid at first (c. 40–50% loss in five weeks), then much slower.

The losses of nitrogen and phosphorus (Fig. 2(b) and (c)) followed a pattern similar to that of the dry-weight loss; the difference between the rate of loss in the clearing and the rate of loss under vegetation was more striking in the case of nitrogen than in that of dry weight or phosphorus.

Potassium (Fig. 2(d)) was lost extremely rapidly from the decomposing leaves at all sites. During the first six weeks potassium was lost somewhat more slowly from leaves placed in the clearing than from those placed under vegetation, but there were no significant differences among sites at the times of the second and third collections of decomposing litter.

Calcium (Fig. 2(e)) and magnesium (Fig. 2(f)) show very different loss characteristics and these were much more variable. The only important variations between different-aged stands for these elements were at the times of the second and third collections, when there was significantly less calcium remaining in decomposing leaves in the mature forest than at the other sites. The mature forest had more organic matter on the soil surface than the young secondary vegetation and this may have insulated the litter bags from contact with the mineral soil. It is probable that the large amount of variation in the calcium and magnesium data reflects variable degrees of contamination of the decomposing litter with mineral soil; the bags were well incorporated into the natural litter and the in-and-out movements of organisms may have introduced appreciable amounts of these two elements. Magnesium dropped during the first interval at all sites, but later behaved unpredictably.

Effects of species decomposing

In Fig. 3 the pooled values are shown for each species, including all six ages of vegetation and both soils. Leaves of four of the species lost weight initially at about the same rate, but those of the palm *Orbignya* decomposed about 20% more slowly. For the four

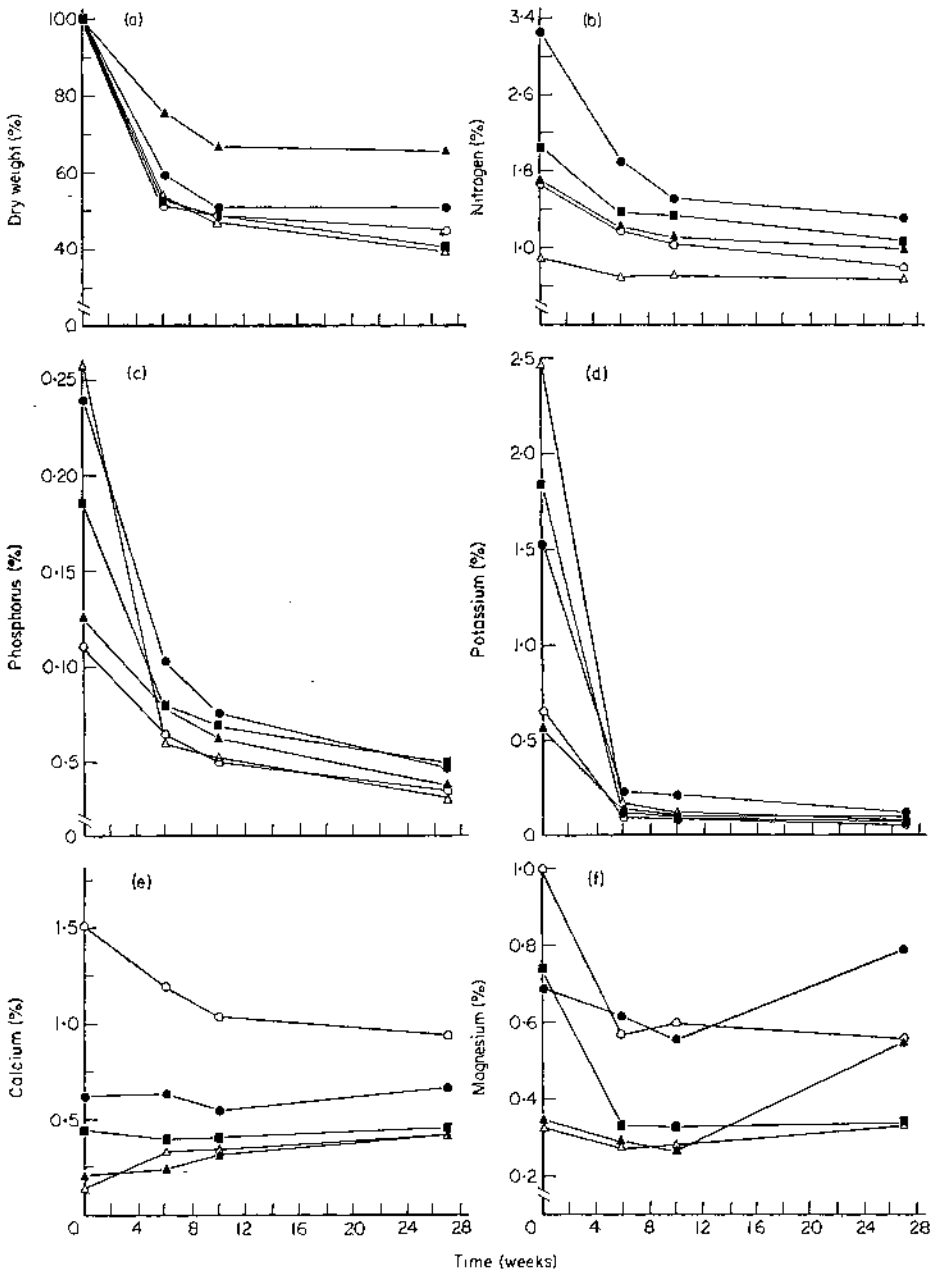


FIG. 3. Losses during decomposition of five species: *Heliconia latispatha* (■), *Trema micrantha* (○), *Paspalum fasciculatum* (Δ), *Cochlospermum vitifolium* (●) and *Orbignya cohune* (▲). Each point represents a mean of twenty-four values: two samples from six ages of vegetation on two soils. The values plotted for the mineral nutrients represent the concentrations that would have been present if there had been no loss of dry weight.

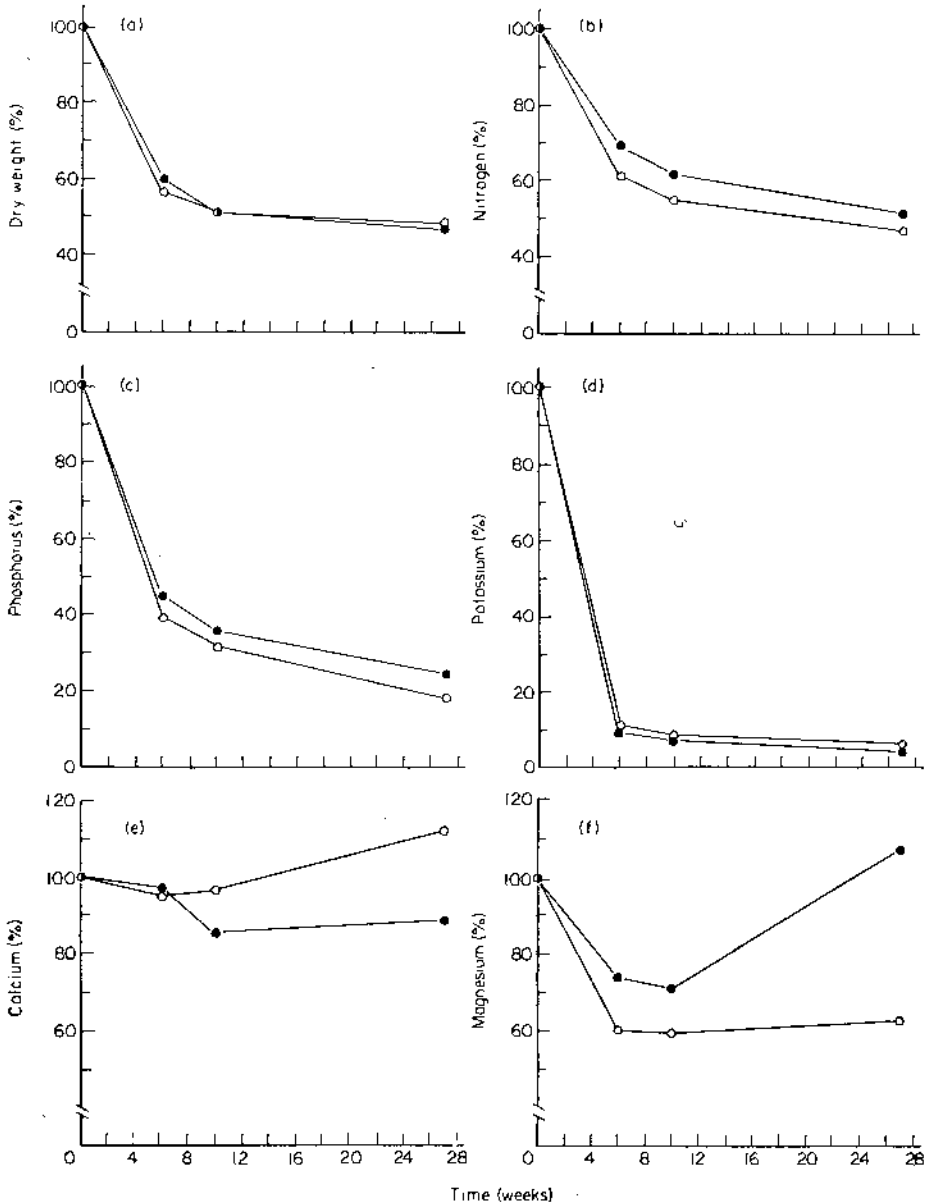


FIG. 4. Losses during decomposition on two soil types: alluvial (●) and upland (○). Each point represents a mean of sixty values: two samples of five species under six ages of vegetation. The values plotted are the percentages of the amounts present at t_0 ; the mean concentrations at t_0 are given in the legend to Fig. 2.

species which decomposed most rapidly 50% weight-loss occurred in about ten weeks.

The five species had very different initial nitrogen concentrations, ranging from *c.* 0.9% in *Paspalum* to *c.* 3.3% in *Cochlospermum*. As decomposition proceeded, however, the nitrogen contents of the five species became increasingly similar (Fig. 3(b)).

The loss of phosphorus (Fig. 3(c)) followed a pattern very similar to that of the nitrogen

loss. Initial phosphorus concentrations among the five species were quite disparate, ranging from 0.11% in *Trema* to almost 0.27% in *Paspalum*.

Potassium was lost extremely rapidly from all species (Fig. 3(d)). The changes in calcium and magnesium for each of the five species (Figs 3(e) and (f)) are rather variable, possibly due to contamination with mineral soil, as indicated above. *Trema* lost about 30% of its initial calcium content during the first ten weeks and *Trema* and *Heliconia* both lost about half of their initial magnesium contents during the first six weeks after the onset of decomposition. The other species showed no clear trends, and their calcium and magnesium contents did not decrease appreciably over the six-month period.

Effects of soil type

The water levels at the upland and alluvial sites were quite different; water often stood on the surface of the alluvium in the rainy season and at certain periods it completely covered many of the litter bags.

In Fig. 4 the values shown represent means of pooled data consisting of all values from the five species and six ages of vegetation on each soil type. The changes in dry weight (Fig. 4(a)) were essentially identical on alluvial and upland soils despite the great differences in water relations.

Nitrogen was lost more rapidly from leaves decomposing on the upland soil (Fig. 4(b)). Only the differences in nitrogen remaining after forty-two days and seventy days were statistically significant ($P < 0.05$).

Phosphorus was also lost somewhat more rapidly on the upland soil (Fig. 4(c)) but only the difference at the time of the final collection was significant.

In contrast, potassium was lost slightly more rapidly on the alluvial soil, though the difference was significant only at the time of the final collection. Even then the difference was only c. 0.03% dry weight—an inconsequential amount.

Decomposing leaves did not lose significant amounts of calcium (Fig. 4(e)) on either soil type. The magnesium content dropped sharply during the first six weeks of decomposition on the upland soil and remained about the same thereafter (Fig. 4(f)). The magnesium content of the decomposing leaves on the alluvial soil also dropped at first, but later increased to values near the initial content.

DISCUSSION

Litter fall and nutrient return

The amount of litter fall and estimated nutrient return for each stand studied is shown in Table 2, together with data from other tropical and subtropical forests. Four additional investigators have reported annual litter fall data (but not nutrient returns) from tropical forests. Jenny, Gessel & Bingham (1949) measured litter fall in three Colombian forests and reported values of 8.5, 10.1 and 12.1 t ha⁻¹. Mitchell (cited by Bray & Gorham 1964) reported values ranging from 8.3 to 14.4 t ha⁻¹ for three secondary forests and 5.5–7.2 t ha⁻¹ for three mature forests, all in Malaya. Madge (1965) reported a litter fall of 5.6 t ha⁻¹ for a Nigerian forest, while Hopkins (1966) measured leaf fall (other litter components were discarded) in three other Nigerian forests and reported values of 4.5, 4.7 and 7.2 t ha⁻¹. The Guatemalan data, therefore, fall within the range of values reported for other tropical and subtropical forests.

The litter production data from the study area underestimate the true values due to the

Table 2. The amounts of dry matter ($t\ ha^{-1}\ yr^{-1}$) and mineral nutrients ($kg\ ha^{-1}\ yr^{-1}$) returned via litter fall in some tropical and subtropical forests

Source	Location	Number of sites	Age of vegetation (years)	Dry weight	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Landelot & Meyer (1954)	Zaire	3	Mature	12.3-15.3*	154-224	7-9	48-87	84-105	44-53
		1	Young secondary	14.9*	140	4	104	124	43
Nye (1961)	Ghana	1	40	10.5	199	7.3	68	206	45
Klinge & Rodrigues (1968)	Brazil	1	Mature	7.3	106	2.1	13	18	13
Singh (1968)	India	5	Mature (disturbed)	1.0-6.2	18-54	<1-28	6-31	15-184	44-30
Bernhard (1970)	Ivory Coast	4	Mature	7.2-13.4	104-170	4.2-13.6	26-81	61-105	22-51
This study	Guatemala	1	1	4.6	74	3.2	11	71	40
		1	3	5.8	97	3.7	17	81	53
		1	4	6.1	103	4.1	11	40	50
		1	5	6.5	89	3.0	12	56	55
		1	6	8.0	142	5.9	20	151	35
		1	9	8.0	144	4.8	12	55	94
		1	14	10.0	144	6.6	24	212	35
		1	Mature	9.0	169	5.8	20	88	64

* Air-dried.

decomposition which occurred during the long intervals between the third and fourth and the fourth and fifth collections. The results of the decomposition study, however, indicate that the rate of decomposition was not greatly affected by the age of the vegetation, so the values are all low by approximately the same percentage. Ten to fifteen per cent of the litter which fell into the collection baskets probably decomposed before it was collected.

Because of between-basket variation, the litter fall in the fourteen-year-old stand did not differ significantly from that in the mature forest, even though the mean was *c.* 10% higher in the younger stand. However, other investigators (e.g. Mitchell cited above; Laudelot & Meyer 1954) have reported higher litter-fall values from secondary forests than from nearby mature forests in the tropics. The secondary stand reported by Laudelot & Meyer (1954) was composed primarily of *Musanga cecropioides* R.Br., an African ecological equivalent of the neotropical *Cecropia peltata* which was an important component of the fourteen-year-old Guatemalan stand; the two stands are therefore likely to be structurally comparable.

Litter fall represents a portion of net primary production. In the lowland humid tropics, successional forests tend to contain more deciduous species than are found in mature forests. Furthermore, successional vegetation is undergoing changes in species composition; entire individuals, including leaves, stems and trunks, contribute to the litter fall. These factors might combine to result in an 'overshoot' of litter production during succession. If the second-order polynomial used to describe the relationship between age of vegetation and litter production (Fig. 1) is correct, litter production might be expected to peak at *c.* twenty-one years, then decline to the level of the mature forest at *c.* thirty-one years.

Nitrogen is returned at a rate greater than twice that reported for most temperate forests (Rodin & Bazilevich 1965). This is due, in part, to the higher rate of leaf fall in tropical areas and, in part, to the higher concentration of nitrogen in leaf litter from tropical forests. Nye (1961) suggested that this tropical/temperate difference may be due to the translocation of nitrogen out of the leaves of most temperate species preceding leaf fall; the species he studied in Ghana did not show corresponding decreases in the nitrogen content of the leaves preceding abscission.

Nitrogen return did not decrease with age of vegetation, suggesting that nitrogen fixation and/or immobilization by vegetation does not reach a maximum during early succession. When vegetation is felled and burned in preparation for shifting agriculture, most of the nitrogen in the vegetation is lost. This element undergoes great variation in the amount present in the vegetation and soil through the cycle of mature forest, planted field and the succession back to mature forest.

The annual return of phosphorus followed a pattern similar to the amount of leaf fall.

The annual return of potassium was quite variable among the sites and was not well correlated with age. The potassium return was certainly underestimated due to the rapidity with which potassium is leached from the litter. The samples upon which the analyses were based represent litter fall over three weeks, during which time considerable potassium was undoubtedly lost from the fallen litter. The actual potassium returns, therefore, may be two to four times greater than the amounts shown in Table 2.

The annual returns of calcium and magnesium were not well correlated with the age of vegetation, but the magnesium return was much less variable than the return of calcium. The range of values reported for the Guatemalan sites encompasses values reported for most other tropical forests except those on the very acid and cation-poor Amazonian soils (Table 2).

Decomposition

Many authors (e.g. Melin 1930; Broadfoot & Pierre 1939; Bartholomew *et al.* 1953) have reported that species with high initial nitrogen contents decompose more rapidly than species low in nitrogen. However Singh (1969) attempted to correlate various chemical constituents of tropical tree species with their rates of decomposition and concluded that numerous chemical characteristics interact to affect the rate of leaf breakdown. Of the species studied in Guatemala, *Cochlospermum* had the highest initial nitrogen content (3.28%), yet it decomposed more slowly than any of the other species except the palm *Orbignya*. The slow decomposition of whole *Cochlospermum* leaves may have been due to the inclusion of the decay-resistant petioles in the decomposition bags. Lignin is slow to decompose (Blow 1955) and is probably in high concentration in the petiole, thus countering the effect of overall high nitrogen. For many tropical species the petiole constitutes more than half of the total dry weight of the leaf and cannot, therefore, be ignored when determining rates of decomposition and release of mineral nutrients.

Bartholomew *et al.* (1953) found that *Panicum* decomposed more rapidly than did any of the tree species included in their study in the Congo region and they attributed the rapid decomposition of the grass to the action of termites. Termite action in the litter at the Guatemalan sites, however, was confined almost entirely to wood and *Paspalum* did not lose weight or mineral nutrients faster than the tree species included in the study. Termites apparently do not play as great a role in the breakdown of leaf litter in the study area as they do in some African ecosystems.

Orbignya decomposed more slowly than the other species and was the only mature-forest species studied. Tree leaves from mature forests in the humid tropics tend to be coriaceous. Heath & Arnold (1966) found that hard-textured 'sun' leaves were less susceptible to breakdown by soil organisms than soft-textured 'shade' leaves. Singh (1969) measured decomposition of ten subtropical forest species and found that species with high lignin content decomposed more slowly than species which were low in lignin. The slow breakdown of *Orbignya* may simply reflect a difference due to the structural characteristics of the particular species; it may also, however, reflect a more general difference between the durability of leaves characteristic of mature forest species and the decomposability of the soft-textured leaves which characterize successional species.

Differences in decomposition rates under the various successional stages were minimal and where such differences were observed they were not sequential with regard to the age of fallow, i.e. decomposition rates did not increase or decrease as the age of the vegetation increased. Differences among stands apparently reflect differences in individual sites, such as soil differences, which are not necessarily related to succession.

Decomposition did, however, consistently and significantly occur more slowly in the cleared areas than under vegetation. References are often encountered in the popular literature which point out the danger of clearing tropical soils due to the increased decomposition of organic matter, supposedly because of its rapid oxidation. Although organic matter is reduced by cultivation, or anything else which reduces the organic inputs to the system, the results of this study indicate that decomposition is retarded by removal of the vegetation. A cleared area in the tropics is a harsh environment, subject to drying during the day and exhibiting a wide daily range in temperature. Such conditions are undoubtedly more rigorous for decomposer organisms than those found in the litter beneath a vegetative cover. Madge (1969) found similar results when comparing decomposition rates in a tropical forest with rates in a tropical savanna. The cleared areas used

in this study acted essentially as microcosms of Madge's (1969) much larger savanna ecosystem and the overall effects of clearing, exposure, drying and moisture fluctuations retarded decomposition in both instances. Decomposition in the tropics is primarily a biological process and is enhanced by the presence of vegetation.

The upland serpentine-derived soils at Murcielagos are undoubtedly low in available nitrogen and phosphorus, and the leaves used in the decomposition study, which had been gathered from plants growing on the alluvial soil, constituted a concentrated source of these elements. The bags on the upland soils were so heavily invaded by roots that it was often necessary to cut the roots in order to lift the bags. This suggests that the higher loss-rates of nitrogen and phosphorus on the upland soils may have been caused by direct uptake by the vegetation, perhaps mediated by mycorrhizal fungi as suggested by McClean (1919) and Went & Stark (1968). If it were a case of more rapid decomposition on the upland soil, weight-loss would also have been higher there than on the alluvium, but that was not the case.

Potassium was lost somewhat more rapidly on the alluvium than on the upland soils, probably because the alluvial plain is a wetter environment than the upland. The abundant moisture might also facilitate loss through base exchange in the presence of abundant calcium and magnesium on the limestone-derived alluvium.

ACKNOWLEDGMENTS

Christopher Hempstead, owner of Murcielagos Farm, generously provided the field sites, living facilities and logistical support in Guatemala. Dr S. C. Snedaker assisted with the field and laboratory work while Dr H. Popenoe and Dr P. J. Grubb provided useful comments on early versions of the manuscript. Financial support was provided by the University of Florida's Center for Tropical Agriculture. Computer time was provided by the Northeast Regional Data Center at the University of Florida.

SUMMARY

The amounts of litter fall and rates of leaf decomposition were measured in young second-growth stands and in mature seasonally deciduous forests in the lowlands of eastern Guatemala (15°30'N, 89°10'W). The dry weights and concentrations of nitrogen, phosphorus, potassium, calcium and magnesium were determined. Litter fall increased with increasing age of vegetation, to a maximum of 10 t ha⁻¹ yr⁻¹ produced by a fourteen-year-old stand; this was not significantly different from the litter fall in mature forest nearby. The decomposition of leaves from five species (*Cochlospermum vitifolium*, *Heliconia latispatha*, *Orbignya cohune*, *Paspalum fasciculatum* and *Trema micrantha*) was measured under six ages of vegetation (0, 3, 6, 9 and 14 years, plus mature forest) and on two soil-types: alluvial and serpentine/limestone-derived upland. Four of the species were successional and their leaves decomposed more rapidly than those of the one mature-forest species used: *Orbignya cohune*, a palm. Decomposition occurred at about the same rate under all ages of vegetation, except that it was significantly slower on sites which were cleared of all vegetation. The rate of loss of dry matter did not differ between the alluvial and upland soils, but the losses of nitrogen and phosphorus were more rapid on the depauperate upland soil and the vegetation may actively remove these elements from the litter.

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(Received 15 July 1975)