

Decomposition and Nutrient Release Patterns of the Leaves of Three Tropical Legumes¹

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ABSTRACT

Information on decomposition and nitrogen release patterns of tropical legumes is scarce despite the important role of legumes in agroforestry systems. Decomposition patterns of the leaves of three tropical legumes *Inga edulis* Mart., *Cajanus cajan* (L.) Millsp., and *Erythrina* sp. were determined by a litterbag study in an alley cropping experiment conducted in the Peruvian Amazon. The leaflets of the three species had similar nitrogen concentrations but different lignin and soluble polyphenolic concentrations. *Inga* and *Cajanus* decomposed at similar rates ($k = 0.91$ and 1.72 yr⁻¹, respectively) and had similar polyphenolic concentrations but differed in lignin. *Erythrina* had the lowest concentration of polyphenolics and decomposed the fastest ($k = 3.45$ yr⁻¹). Polyphenolics appeared to influence rates of decomposition more than percent nitrogen or percent lignin. It is proposed that the polyphenolics bind to N in the leaves forming compounds resistant to decomposition. These compounds may be precursors to stable forms of nitrogen in soil organic matter. Rates of nutrient loss followed the general trend potassium > phosphorus, nitrogen, and magnesium > calcium. It is apparent from this study that not all leguminous leaves decompose and release nitrogen quickly, despite high nitrogen concentrations in the leaves. Nitrogen release by legumes with high polyphenolic concentrations will be slower than that by legumes with low polyphenolic concentrations and has important implications to nitrogen cycling and the selection of legumes for agroforestry systems.

RESUMEN

Conocimientos acerca de los patrones de descomposición y mineralización de nitrógeno en leguminosas tropicales son escasos a pesar del importante papel que estas leguminosas juegan en sistemas agroforestales. Los patrones de descomposición de las hojas de tres leguminosas tropicales, *Inga edulis* Mart., *Cajanus cajan* (L.) Millsp., y *Erythrina* sp. fueron determinadas en un estudio con bolsas de hojarasca en un experimento de cultivos en callejones en la Amazonía del Perú. Las hojas de las tres especies tenían contenidos similares de nitrógeno, pero diferentes contenidos de lignina y polifenólicos solubles. Las constantes de descomposición, k , fueron 0.91, 1.72 y 3.47 por año para *I. edulis*, *C. Cajan* y *Erythrina* sp, respectivamente. Aparentemente, los polifenólicos influyen las tasas de descomposición más que el contenido de nitrógeno o de lignina. *Inga* y *Cajanus* se descompusieron a tasas similares y tenían contenidos similares de polifenólicos más rápida. Se propone que los polifenólicos forman compuestos con el nitrógeno de las hojas que son resistentes a la descomposición. Dichos compuestos pueden ser precursores de formas estables de nitrógeno en la materia orgánica del suelo. La mineralización de nutrientes siguió un patrón similar a la descomposición. Las tasas de pérdidas de nutrientes de las hojas siguen. La tendencia potasio > fósforo > nitrógeno, y magnesio > calcio. Este trabajo indica que no todas las hojas de leguminosas se descomponen y mineralizan nitrógeno rápidamente, pese a altas concentraciones de nitrógeno en las hojas. La mineralización de nitrógeno por leguminosa con altos contenidos de polifenólicos será más lenta que aquellos con altos contenidos de polifenólicos. Esta conclusión lleva importantes implicaciones al reciclaje de nitrógeno y a la selección de leguminosas para sistemas agroforestales.

LEGUMINOUS TREES AND SHRUBS are commonly used in agroforestry systems in the humid tropics. Well-known examples are interplantings of *Erythrina* sp. and *Inga* in coffee and cacao plantations in Latin America (Aranguren *et al.* 1982a, b; Bornemisza 1982; Santana & Cabala-Rosand 1982). The trees provide shade and also serve as a source of nitrogen through litterfall and periodic prunings. In alley cropping, rows of leguminous trees are pruned every

three to six months and the prunings are used as a mulch or green manure for a food crop growing between the rows (Kang *et al.* 1981).

It is assumed that the prunings and litterfall from leguminous plants offer a readily available source of nitrogen. Plant materials with high nitrogen content, such as in nitrogen-fixing legumes, are considered to be of high resource quality to microorganisms and they decompose and release nitrogen quickly (Crowther & Mirchandani 1931, Miller *et al.* 1936, Schofield 1945, Harmsen & van Schreven 1955, Weeraratna 1979). Certain plant constituents, however, can modify the quality of the plant

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material, slowing decomposition and the release of nitrogen (Handley 1961, Swift *et al.* 1979). Plant materials with high lignin concentration decompose more slowly than those with low lignin concentration (Tenney & Waksman, 1929, Melillo *et al.* 1982). Lignin may also immobilize nitrogen during decomposition (Berg & Staaf 1981, Melillo *et al.* 1982, Berg & McLaugherty 1987). Immobilization refers to the processes whereby decomposer organisms utilize and accumulate nutrients from the soil solution. If there is net immobilization the nutrient content of the decomposing material exceeds 100 percent of the original, this process usually occurs if the initial nitrogen content of the tissue was low, or nutrients were in an unavailable form.

Polyphenolics can also retard decomposition and nitrogen release by binding to nitrogen-containing compounds in the plant material, forming resistant complexes. Polyphenolics can also slow decomposition by inhibiting enzyme action (Swain 1979). There is increasing evidence that some legumes with high polyphenolic concentration decompose and release nitrogen more slowly than would be predicted based solely on their nitrogen concentration (Vallis & Jones 1973, Palm 1988) and may in fact show prolonged phases of nitrogen immobilization.

The use of high versus low quality legumes in agroforestry systems could be important to nitrogen dynamics and management practices. The purpose of this study was to investigate the decomposition and nitrogen release patterns from leaves of leguminous trees with differing lignin and polyphenolic contents. The hypothesis was that leaves higher in lignin concentration or lignin-to-nitrogen ratio would decompose and release nitrogen more slowly than those with lower concentrations. Because leguminous prunings can also serve as a source of other nutrients to crop plants, the release of phosphorus, calcium, magnesium, and potassium from decomposing plant material was also investigated.

METHODS

SITE DESCRIPTION.—The study was located at the Yurimaguas Experiment Station in the upper Amazon Basin of Peru (76°05'W, 5°45'S, 180 m elevation). The area has a mean annual temperature of 26°C and annual rainfall of 2200 mm. Monthly rainfall exceeds 200 mm in all months except June, July, August, and September which have closer to 100 mm.

The experiment was conducted on an acid soil of an upland terrace. The soil was a fine loamy,

siliceous, isohyperthermic Typic Paleudult. Clay content in the top 15 cm averaged 27 percent. Kaolinite is the predominant mineral in the clay fraction in the upland soils of the region (Tyler 1975). The topsoil had an effective cation exchange capacity of 6 meq per 100 g of soil, pH value of 4.6, and aluminum saturation of 78 percent. Total carbon and nitrogen in the topsoil were 1.10 and 0.11 percent, respectively.

EXPERIMENTAL DESIGN AND MEASUREMENTS.—*Field study:* The litterbag study was conducted as part of a larger alley cropping experiment designed to test the effect of species of mulch and mulch rates on nitrogen cycling. The design of the alley cropping experiment used species of mulch (*Inga edulis*, *Cajanus cajan*, *Erythrina* sp.) as the main plot treatment and mulch rate (0, 3.3, 6.7 t⁻¹ha⁻¹crop⁻¹) as the subplot treatment. Treatments were arranged in three blocks with two replications per block, only the 3.3 t⁻¹ha⁻¹ subplots were used in the litterbag study.

The three woody leguminous species, *Inga edulis* Mart, *Cajanus cajan* (L.) Millsp., and *Erythrina* sp., used in the study are commonly found in agroforestry systems in the humid tropics. Leaves for the litterbags were hand picked from trees in an alley cropping experiment and included a mixture of new and old leaves. Because *Inga edulis* has a large, highly lignified central rachis, only leaflets from all three species were used in the litterbag study to avoid confounding nitrogen dynamics and mulch quality parameters. For each species, 15 g of air-dried leaflets were placed in 20 × 20 cm nylon litterbags of 1-mm mesh. Subsamples were oven dried at 70°C to calculate the oven-dry mass.

Sixteen litterbags were placed on the soil surface in November 1985 in each of the subplots containing prunings of the same species. One litterbag was collected from each subplot (providing a total of six replicates for each species) at one, two, four, six, and eight weeks and then every four weeks. Collections were discontinued at week 20 for *Erythrina* and at week 32 for the other two species. Leaves remaining in the litterbags at each collection time were cleaned by hand to remove roots, organic debris, and mineral soil. The cleaned samples were oven dried at 70°C, weighed, and ground. Subsamples were ashed (described in next section) to correct for contamination from the mineral soil. Data are presented as percent original leaf mass remaining.

Laboratory analyses: Leaflets, ground to 1 mm, were analyzed for initial nutrients, lignin, soluble poly-

TABLE 1. Initial nutrient, lignin, and polyphenolic concentrations (standard error of the mean) of the leguminous leaves used in the litterbag study.

Species	N	P	Ca	Mg	K	Lignin	Poly-phenolics
	%						
<i>Inga edulis</i>	3.18 (.15)	0.22 (.02)	0.74 (.06)	0.17 (.01)	1.25 (.08)	16.3 (1.34)	3.43 (.46)
<i>Cajanus cajan</i>	3.48 (.06)	0.18 (.02)	0.63 (.01)	0.18 (.01)	1.35 (.06)	10.2 (.66)	3.34 (.43)
<i>Erythrina</i> sp.	3.52 (.13)	0.21 (.02)	0.88 (.16)	0.35 (.02)	2.02 (.02)	9.7 (.69)	1.04 (.21)

phenolics, and ash-free dry mass; nutrients were analyzed on oven-dried samples, whereas, air-dried samples were used for the organic constituents. Nitrogen was analyzed by micro Kjeldahl methods using a mixture of K_2SO_4 , H_2SO_4 , and selenium for the digestion step. Phosphorus, potassium, calcium, and magnesium were analyzed by digestion in concentrated H_2SO_4 and 30 percent H_2O_2 . Phosphorus was measured by the molybdate blue method (Olson & Dean 1965) and calcium, magnesium, and potassium by atomic absorption spectrophotometry. Lignin was analyzed by the acid detergent fiber method (Van Soest & Wine 1968). Polyphenolics were extracted in 50 percent aqueous methanol for one hour in a water bath (80°C) and analyzed by the Folin-Denis method as described by King and Heath (1967) and reported as percent tannic acid equivalent. Ash-free dry mass was determined by ashing in a muffle furnace at 550°C for three hours.

The percent of nutrients remaining in the decomposing leaflets at each time was also determined and calculated by multiplying the leaf mass remaining by the nutrient concentrations.

Statistical analyses: Analyses of variance were performed to determine differences in the decomposition and nutrient mineralization patterns of the three species. Species and time were considered as the main effects (Wieder & Lang 1982, Statistical Analysis System 1985). If species by time interactions were found, an analysis of variance was performed for each time interval to examine the decomposition patterns in more detail. Differences were reported as significant if the probability was less than 0.05. Differences between species at each collection time were determined by least significant differences (LSD).

Decomposition and nutrient loss constants, k ,

were determined for dry mass and nutrients for each of the species by the single exponential model, $\bar{x} = e^{-kt}$, where \bar{x} is the proportion of initial mass or nutrient remaining at each time, t , in years (Wieder & Lang 1982). Data from all collection times were used. Decomposition and nutrient loss constants were compared statistically by considering k as the slope for the log form of the equation and performing pairwise t -tests for slopes.

RESULTS

INITIAL CHARACTERISTICS OF LEAVES.—Nitrogen concentrations of the leaflets of the three legumes ranged from 3.18 percent in *Inga* to 3.52 percent in *Erythrina* (Table 1). Phosphorus concentrations were similar for the three species, near 0.20 percent and are high compared to leaves from other tropical trees (Vitousek & Sanford 1986). Potassium, calcium, and magnesium concentrations of *Erythrina* leaflets were generally higher than in the other two species. Lignin and polyphenolic contents in *Inga* were both toward the upper end of the range reported for tropical leaves (Anderson *et al.* 1983). In contrast, *Erythrina* had low contents of both. *Cajanus* had a high polyphenolic content, similar to that of *Inga*, but a low lignin content, similar to that of *Erythrina*.

DECOMPOSITION AND NUTRIENT RELEASE PATTERNS.—*Inga* and *Cajanus* exhibited similar decomposition patterns that were significantly different from that of *Erythrina* (Fig. 1). All three species had a rapid phase of decomposition lasting about one month followed by a slower phase. In *Erythrina* the rapid phase was more pronounced. The overall analysis of variance revealed significant species and time effects for leaf mass remaining but also significant species by time interactions making conclusions about

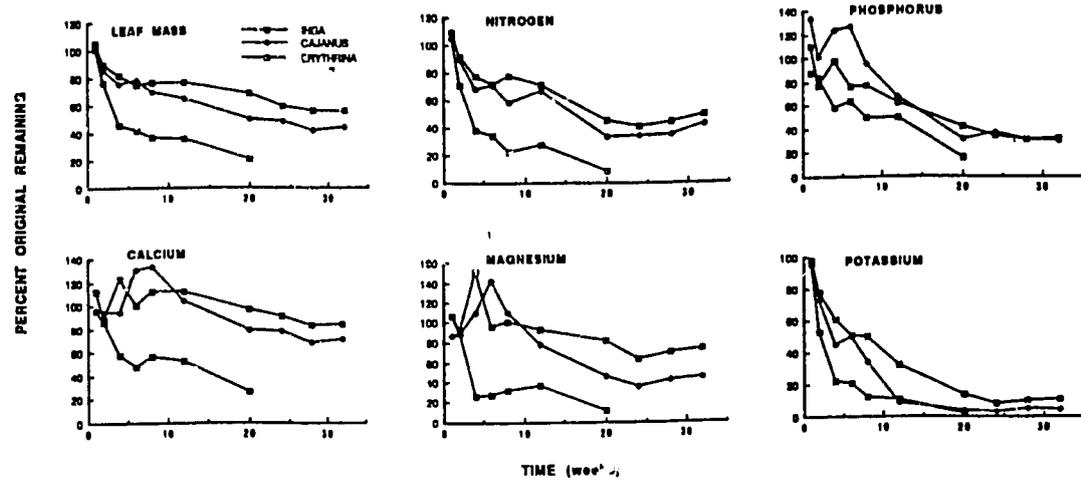


FIGURE 1. Percent of original leaf mass, N, P, Ca, Mg and K remaining with time for decomposing leaves of *Inga edulis*, *Cajanus cajan*, and *Erythrina* sp. Time 0, not shown on graphs, is equal to 100%.

the difference between species unclear (Wieder & Lang 1982). Analysis of variance for each collection time showed that *Inga* and *Cajanus* had a similar proportion of leaf mass remaining at all collection times except week 12, when *Inga* had more. *Erythrina* had significantly less remaining at all times except the first collection period.

A statistical comparison of the decomposition constants supports the observation that *Erythrina* decomposed significantly faster than the other species, while *Cajanus* tended to decompose faster than *Inga* (Table 2). The t_{50} , or time for 50 percent of the material to decompose, were 0.19, 0.47, and 0.76 yr for *Erythrina*, *Cajanus*, and *Inga*, respectively.

Decomposing leaves of *Erythrina*, in general, released nutrients significantly faster than *Inga* and

Cajanus (Fig. 1, Table 2). Analysis of variance by time showed that *Erythrina* lost nitrogen, calcium, magnesium, and potassium significantly faster than the other two species and phosphorus initially faster than *Cajanus*. *Inga* and *Cajanus* showed similar patterns of release for nitrogen and calcium. *Cajanus* released phosphorus more slowly initially than *Inga* but *Inga* released magnesium and potassium more slowly.

Within each species, nutrient loss constants, or k values, for all nutrients except calcium were greater than those for leaf mass (Table 2). The turnover times, $1/k$, of all nutrients were less than one year, except for calcium in *Inga* and *Cajanus* and magnesium in *Inga*. The rate of loss of nutrients from the decomposing leaves followed the general trend potassium > phosphorus, nitrogen, and magnesium

TABLE 2. Decomposition and nutrient loss constants, k , for leguminous leaves as determined by the litterbag method. Letters beside numbers are for comparing k values within a species and letters below numbers are for comparing k values between species. Numbers with similar letters are not significantly different ($P = .05$). Comparisons were made by pairwise t -tests for slopes.

Species	Ash-free dry weight	N	P	Ca	Mg	K
<i>Inga edulis</i>	0.91b b	1.42b b	1.96b b	0.44b b	0.91b c	4.15a b
<i>Cajanus cajan</i>	1.45c b	1.70c b	2.83b ab	0.80d b	1.93c b	5.73a b
<i>Erythrina</i> sp.	3.72b a	5.99b a	4.32b a	3.02b a	4.97b a	9.54a a

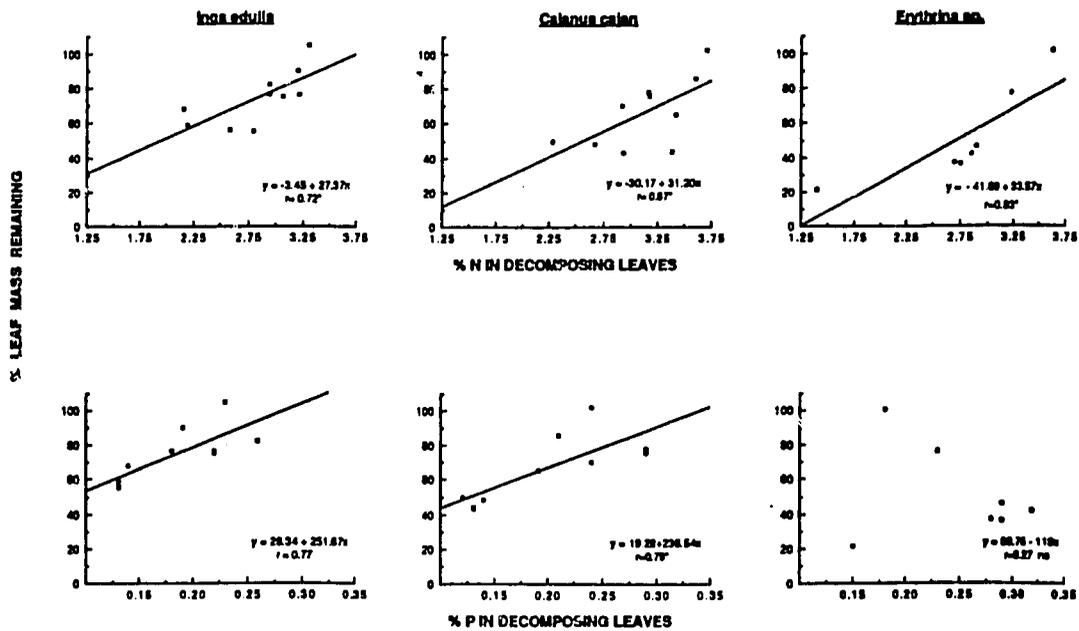


FIGURE 2. Relationship between the percent leaf mass remaining and the percent N and percent P in the decomposing leaves; * significant at $P = 0.05$, NS not significant.

> calcium. An exception to this was that nitrogen tended to be lost more rapidly than phosphorus in *Erythrina*.

There was no significant net immobilization of nitrogen by any of the species (Fig. 1). However, there was a short net immobilization phase of phosphorus in *Cajanus* and longer periods of immobilization of calcium and magnesium in both *Inga* and *Cajanus*. The immobilization phases for phosphorus, calcium, and magnesium follow similar patterns among species, immobilization occurred at week one followed by a net loss at week two and then immobilization again at week four (Fig. 1).

Decomposition was accompanied by a decrease in the nitrogen concentration in the remaining leaf mass in all three species (Fig. 2). *Inga* and *Cajanus* showed a decrease until week 20 when an increase in nitrogen concentration began. Phosphorus concentrations also decreased in *Inga* and *Cajanus* (Fig. 2). *Erythrina* showed a significant increase in phosphorus concentration until week 12 ($r = 0.94$) when there was a significant drop in concentration causing an overall lack of correlation. The faster loss of phosphorus than nitrogen in *Inga* and *Cajanus* resulted in an increase in the nitrogen-to-phosphorus ratio from 15 to greater than 20, following an initial drop to 10 (Fig. 3). In *Erythrina* nitrogen was lost

faster than phosphorus and the nitrogen-to-phosphorus ratio decreased from 17 to less than 10, remaining fairly constant, despite significant changes in both the nitrogen and phosphorus concentrations.

DISCUSSION

Decomposition rate constants were within the range reported for the humid tropics (Anderson *et al.* 1983, Anderson & Swift 1983). Rate constants obtained from the single exponential equation do not always provide the best fit to describe decomposition patterns (Wieder & Lang 1982, Ezcurra & Becerra 1987, Spain & Le Feuvre 1987). However, given the high r^2 values (>0.83) obtained for the three species in this study, the single exponential equation seems reasonable.

Decomposition of leguminous leaves or litter in the tropics has received little attention. The few values reported in the literature indicate high but variable decomposition rate constants, ranging from 1.65 to 8.48 yr^{-1} (Table 3). Both *I. edulis* and *C. cajan* decomposed slower than this reported range for legumes. Meentemeyer (1978) suggested that the quality of the plant material controls the rate of decomposition in the tropics more than climatic

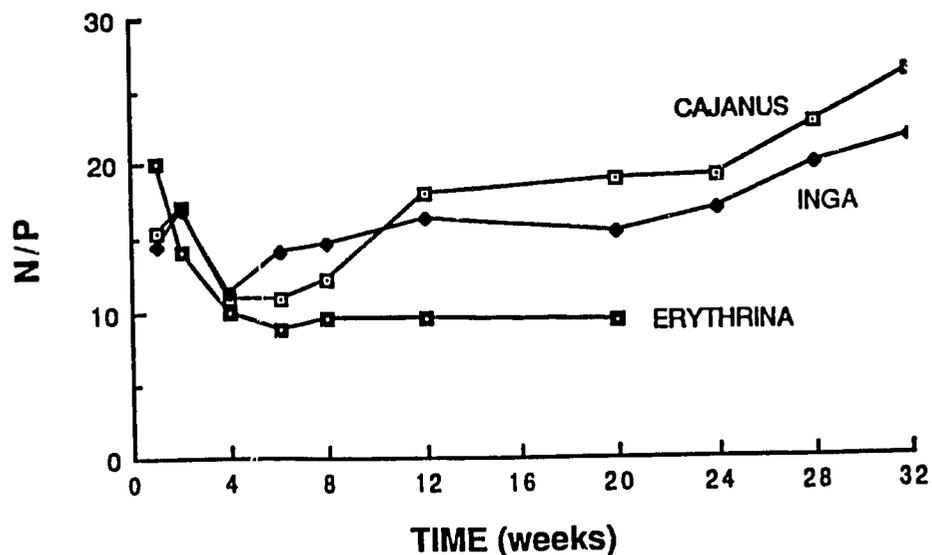


FIGURE 3. The nitrogen-to-phosphorus ratios with time in decomposing leaves of *Inga edulis*, *Cajanus cajan*, and *Erythrina* sp.

factors and that within a site percent lignin is a good predictor of decomposition rates. Neither percent lignin nor lignin-to-nitrogen ratio, as suggested by Melillo *et al.* (1982), were useful in predicting the rates of decomposition in this study. *Erythrina* and *Cajanus* had similar lignin and nitrogen contents yet decomposed at significantly different rates. Of the plant characteristics measured, soluble polyphenolic concentration was most related to rates of decomposition; *Erythrina* with a low polyphenolic

content decomposed twice as fast as *Inga* and *Cajanus*, both of which had higher and similar polyphenolic contents.

The fact that no net nitrogen immobilization took place in this study contrasts sharply with results from temperate regions (Berg & Staaf 1981, Melillo & Aber 1984). The lack of net nitrogen immobilization has been found in other studies in the tropics, even for nonleguminous leaves and litter (Laudelout 1961; Swift *et al.* 1981; Aranguren *et al.*

TABLE 3. Decomposition constants, *k*, for tropical legumes. Values were calculated with exponential equation for decomposition (Wieder and Lang, 1982) using data reported in the literature.

Species	Location	Mean annual		<i>k</i> (yr ⁻¹)	Reference
		Rain- fall (mm)	Tem- pera- ture (°C)		
<i>Gliricidia sepium</i>	Ibadan, Nigeria	1250	23-31	8.48	Yamoah <i>et al.</i> 1986
<i>Flemingia congesta</i>	Ibadan, Nigeria	1250	23-31	3.66	Yamoah <i>et al.</i> 1986
<i>Cassia siamea</i>	Ibadan, Nigeria	1250	23-31	2.17	Yamoah <i>et al.</i> 1986
<i>Lonchocarpus cyanescens</i>	Ibadan, Nigeria	1250	23-31	8.87	Swift <i>et al.</i> 1981
<i>Inga vera</i>	El Verde, Puerto Rico	4000	22	1.65	La Caro and Rudd 1985
<i>Inga</i> sp. and <i>Erythrina</i> (mixed)	Caracas, Venezuela	1200	20	3.01	Aranguren <i>et al.</i> 1982a
<i>Erythrina</i> sp. (mixed with nonlegumes)	Caracas, Venezuela	1200	20	3.81	Aranguren <i>et al.</i> 1982b
<i>Inga edulis</i>	Yurimaguas, Peru	2200	26	0.91	This study
<i>Cajanus cajan</i>	Yurimaguas, Peru	2200	26	1.45	This study
<i>Erythrina</i> sp.	Yurimaguas, Peru	2200	26	3.72	This study

1982a, b; Anderson *et al.* 1983; Upadhyay & Singh 1985) and may even be the norm for the tropics (Vitousek 1984, Vogt *et al.* 1986). No net immobilization was predicted based on the inverse linear regression model of Melillo and Aber (1984) that relates mass loss to the percent nitrogen in the remaining tissue, because there was no increase in the nitrogen concentration of the decomposing leaves (Fig. 2). A decrease in nitrogen concentration in the remaining leaf mass is quite unusual even for leaves showing no net nitrogen immobilization (Laudelout 1961; Aranguren *et al.* 1982a, b; Upadhyay & Singh 1985; Sharma & Ambasht 1987).

Nitrogen release by *Inga* and *Cajanus* levels off at week 20, and coincides with an increase in the nitrogen concentration in the remaining tissue. In the first phase the soluble nitrogen fraction is leached or mineralized. The second phase might be explained by the binding of nitrogen to lignins or polyphenolics in the leaves (Handley 1961, Vallis & Jones 1973, Suberkropp *et al.* 1976, Schlesinger & Hasey 1981, Berg & Staaf 1981, Berg & McClaugherty 1987). The latter explanation is more likely for *Cajanus* given its low initial lignin content; whereas, both are possibilities for *Inga* which has high lignin and high polyphenolic content initially. It would be difficult to distinguish between the two because polyphenolic-nitrogen complexes end up in the same fraction as lignin, an acid-insoluble fraction in most laboratory procedures (Suberkropp *et al.* 1976, Spain & Le Feuvre 1987).

The phosphorus release patterns observed also demonstrate the importance of substrate quality on nutrient dynamics. No long-term phosphorus immobilization occurred but the phosphorus concentration and nitrogen-to-phosphorus ratio in the remaining litter suggest that nitrogen dynamics may influence that of phosphorus, at least in the early stages of decomposition. *Inga*, *Cajanus*, and *Erythrina* began with nitrogen-to-phosphorus ratios of 14, 19, and 16, respectively. Despite high initial levels of phosphorus, all three species showed increased phosphorus concentration in the tissue at week four, resulting in ratios near ten, the ideal ratio for decomposer organisms (Vogt *et al.* 1986). *Cajanus*, which had the highest nitrogen-to-phosphorus ratio, showed a short immobilization phase. The ratios gradually increased to 22 and 25 for *Inga* and *Cajanus*, respectively. The increase was more likely due to the lack of available nitrogen in the leaves toward the end of the study rather than phosphorus limitation. Thus, for these two species, nitrogen may have influenced phosphorus dynamics

early; but later, phosphorus was mineralized independently of nitrogen. This explanation is supported by the faster turnover times for phosphorus than nitrogen for these two species. *Erythrina* maintained a nitrogen-to-phosphorus ratio near ten throughout the course of the study, suggesting that nitrogen was controlling phosphorus dynamics.

Phosphorus immobilization during decomposition has been reported for the tropics (Anderson *et al.* 1983) as well as temperate zones (Schlesinger & Hasey 1981, Melillo & Aber 1984, Schlesinger 1985). It has been suggested that phosphorus immobilization, or an increase in phosphorus concentration in the remaining plant material, occurs where phosphorus is limiting to microbial activity (Melillo & Aber 1984, Schlesinger 1985, Vitousek & Sanford 1986). Schlesinger and Hasey (1981) suggest that carbon-to-phosphorus ratios are important for decomposition of chaparral litter, whereas Vogt *et al.* (1986) imply that nitrogen-to-phosphorus ratios determine whether phosphorus immobilization will occur.

The order of release of the cations, potassium > magnesium > calcium, and the patterns of release are similar to those reported in other studies. The initial immobilization and slow turnover rate of calcium has also been observed both in the tropics and temperate zone (Suarez-Vasquez & Cabrillo-Pachon 1976, Schlesinger & Hasey 1981, Swift *et al.* 1981, Anderson *et al.* 1983) and is generally attributed to accumulation of calcium oxalate in the fungi that colonize decomposing leaf tissue (Cromack *et al.* 1975). This immobilization of calcium during decomposition has interesting implications for crop management in that calcium deficiencies may be created, particularly on acid, calcium-poor soils. Potassium was released the fastest of all the nutrients, at a rate faster than the leaves decomposed. This trend supports claims that leaching is the primary process influencing losses of potassium (Swift *et al.* 1981).

The results from this study suggest that decomposition and nitrogen release of leguminous leaves are influenced by the polyphenolic concentration of the leaves. Leaves low in polyphenolic content release nitrogen more rapidly than those high in polyphenolic content, which show a rapid initial release followed by a slow release. It is proposed that polyphenolics bind to nitrogen forming resistant complexes, slowing decomposition and nitrogen release. Polyphenolic content may, therefore, be an important factor to consider when selecting legumes for agroforestry systems. Legumes low in polyphenolics

will provide a rapid flush of nitrogen mineralization and may, therefore, be a good choice for use with annual crops that require large amounts of nitrogen for short periods of time. Nitrogen release by legumes higher in polyphenolic content will be slower and over a longer time period and may be the better choice for tree-production systems. Although little consideration has been given to the quality of leguminous mulches, it may be particularly important as legumes are used in agroforestry systems on more marginal, acid soils. The polyphenolic content is generally higher in plants growing on poor soils (McVey *et al.* 1978), even within the same species (Muller *et al.* 1987), and may have important implications to nitrogen cycling on these soils.

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LITERATURE CITED

- ANDERSON, J. M., AND M. J. SWIFT. 1983. Decomposition in tropical forests. In S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). Tropical rain forest: ecology and management, pp. 287-309. Blackwell Scientific Publications, Oxford, England.
- , J. PROCTOR, AND H. W. VALLACK. 1983. Ecological studies in four contracting rain forests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter. *J. Ecol.* 71: 503-527.
- ARANGUREN, J., G. ESCALANTE, AND R. HERRERA. 1982a. Nitrogen cycle of tropical perennial crops under shade trees: I. Coffee. In G. P. Robertson, R. Herrera, and T. Rosswall (Eds.). Nitrogen cycling in ecosystems of Latin America and the Caribbean, pp. 247-258. Martinus Nijhoff/Dr W. Junk, The Hague, Netherlands.
- , AND ———. 1982b. Nitrogen cycle of tropical perennial crops under shade trees: II. Cocoa. In G. P. Robertson, R. Herrera, and T. Rosswall (Eds.). Nitrogen cycling in ecosystems of Latin America and the Caribbean, pp. 259-270. Martinus Nijhoff/Dr W. Junk, The Hague, Netherlands.
- BERG, B., AND C. McCLAUGHERTY. 1987. Nitrogen release from litter in relation to the disappearance of lignin. *Biogeochemistry* 4: 219-224.
- , AND H. STAAF. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In F. E. Clark and T. Rosswall (Eds.). Terrestrial nitrogen cycles, pp. 163-178. *Ecol. Bull.* Vol. 33. Stockholm, Sweden.
- BORNEMISZA, E. 1982. Nitrogen cycling in coffee plantations. In G. P. Robertson, R. Herrera, and T. Rosswall (Eds.). Nitrogen cycling in ecosystems of Latin America and the Caribbean, pp. 241-246. Martinus Nijhoff/Dr W. Junk, The Hague, Netherlands.
- CROMACK, K., JR., R. L. TODD, AND C. D. MONK. 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. and Biochem.* 7: 265-268.
- CROWTHER, E. M., AND T. J. MIRCHANDANI. 1931. Winter leaching and the manurial value of green manures and crop residues for winter wheat. *J. Agric. Sci.* 21: 493-525.
- EZCURRA, E., AND J. BECERRA. 1987. Experimental decomposition of litter from the Tamaulipan Cloud Forest: a comparison of four simple models. *Biotropica* 19: 290-296.
- HANDLEY, W. R. C. 1961. Further evidence for the importance of residual protein complexes on litter decomposition and the supply of nitrogen for plant growth. *Plant Soil* 15: 37-73.
- HARMSEN, G. W., AND D. A. VAN SCHREVEN. 1955. Mineralization of organic nitrogen in soil. *Adv. Agron.* 7: 299-398.
- KANG, B. T., G. F. WILSON, AND L. SIPKENS. 1981. Alleycropping maize (*Zea mays* L.) and leucaena (*Leucaena leucocephala* Lam.) in southern Nigeria. *Plant Soil* 63: 165-179.
- KING, H. G. C., AND G. W. HEATH. 1967. The chemical analysis of small samples of leaf material and the relationship between the disappearance and composition of leaves. *Pedobiologia* 7: 192-197.
- LACARO, F., AND R. L. RUDD. 1985. Leaf litter disappearance rates in Puerto Rican montane rain forests. *Biotropica* 17: 269-276.
- LAUDELOUT, H. 1961. Dynamique des sols tropicaux et les differents systems de jachere, 126 pp. UN-FAO Report FAO, Rome, Italy.
- McVEY, D., P. G. WATERMANN, C. N. MBI, J. S. GARTLAN, AND T. T. STRUHSAKER. 1978. Phenolic content of vegetation in two African rain forests: ecological interpretations. *Science* 202: 61-64.

- MEENTEMEYER, V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59: 465-472.
- MELILLO, J. M., AND J. D. ABER. 1984. Nutrient immobilization in decaying litter: an example of carbon-nutrient interactions. In J. H. Cooley and F. B. Golley (Eds.). *Trends in ecological research for the 1980s*, pp. 193-215. Plenum Publishing Corporation, New York, New York.
- , AND J. F. MURATORE. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63: 621-626.
- MILLAR, H. C., F. B. SMITH, AND P. E. BROWN. 1936. The influence of organic matter on nitrate accumulation and the base exchange capacity of Dickinson fine sandy loam. *J. Am. Soc. Agron.* 28: 856-866.
- MULLER, R. N., P. J. KALISZ, AND T. W. KIMMERER. 1987. Intraspecific variation in production of astringent phenolics over a vegetation-resource availability gradient. *Oecologia* 72: 211-215.
- OLSON, S. R., AND L. A. DEAN. 1965. Phosphorus. In C. A. Black (Ed.). *Methods of soil analysis. Part 2. Chemical and biological properties*, pp. 1035-1058. American Society of Agronomy, Madison, Wisconsin.
- PALM, C. A. 1988. Mulch quality and nitrogen dynamics in an alley cropping system in the Peruvian Amazon. Ph.D. Thesis, North Carolina State University, Raleigh, North Carolina.
- SANTANA, M. B. M., AND P. CABALA-ROSAND. 1982. Dynamics of nitrogen in a shaded cacao plantation. In G. P. Robertson, R. Herrera, and T. Rosswall (Eds.). *Nitrogen cycling in ecosystems of Latin America and the Caribbean*, pp. 271-282. Martinus Nijhoff/Dr. W. Junk, The Hague, Netherlands.
- SCHLESINGER, W. H. 1985. Decomposition of chaparral shrub foliage. *Ecology* 66: 1352-1359.
- , AND M. H. HASEY. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62: 762-774.
- SCHOFIELD, J. L. 1945. A comparison of soil nitrate nitrogen values under bare fallow and after ploughing in various perennial tropical legumes and cowpeas. *Queensl. J. Agric. Sci.* 2: 170-189.
- SHARMA, E., AND R. S. AMBASHT. 1987. Litterfall, decomposition and nutrient release in an age sequence of *Alnus nepalensis* plantation stands in the eastern Himalaya. *J. Ecol.* 75: 997-1010.
- SPAIN, A. V., AND R. P. LE FEUVRE. 1987. Breakdown of four litter of contrasting quality in a tropical Australian rainforest. *J. Appl. Ecol.* 24: 279-288.
- STATISTICAL ANALYSIS SYSTEM. 1985. SAS User's Guide. SAS Institute, Cary, North Carolina.
- SUAREZ-VASQUEZ, S., AND I. F. CARRILLO-PACHON. 1976. Descomposicion biologica de leguminosas y otros materiales de la zona cafetera Colombiana. *Cenicafe* 27: 67-77.
- SUBERKROPP, K., G. L. GODSHALK, AND M. J. KLUG. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. *Ecology* 57: 720-727.
- SWAIN, T. 1979. Tannins and lignins. In G. A. Rosenthal and D. H. Janzen (Eds.). *Herbivores: their interactions with secondary plant metabolites*, pp. 657-822. Academic Press, New York, New York.
- SWIFT, M. J., O. W. HEAL, AND J. M. ANDERSON. 1979. Decomposition in terrestrial ecosystems. *Studies in ecology*, Vol. 5. University of California Press, Berkeley, California.
- , A. RUSSELL-SMITH, AND T. J. PERFECT. 1981. Decomposition and mineral-nutrient dynamics of plant litter in a regenerating bush-fallow in sub-humid tropical Africa. *J. Ecol.* 69: 981-995.
- TENNEY, F. G., AND S. A. WAKSMAN. 1929. Composition of natural organic materials and their decomposition: IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. *Soil Sci.* 28: 55-84.
- TYLER, E. J. 1975. Genesis of the soils within a detailed soil survey area in the upper Amazon Basin, Yurimaguas, Peru. Ph.D. Dissertation, North Carolina State University, Raleigh, North Carolina.
- UPADHYAY, V. P., AND J. S. SINGH. 1985. Nitrogen dynamics of decomposing hardwood leaf litter in a central Himalayan forest. *Soil Biol. Biochem.* 17: 827-830.
- VALLIS, I., AND R. J. JONES. 1973. Net mineralization of nitrogen in leaves and leaf litter of *Desmodium intortum* and *Phaseolus atropurpureus* mixed with soil. *Soil Biol. Biochem.* 5: 391-398.
- VAN SOEST, P. J., AND R. H. WINE. 1968. Determination of lignin and cellulose in acid-detergent fiber with permanganate. *J. Assoc. Off. Anal. Chem.* 51: 780-785.
- VITOUSEK, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- , AND R. L. SANFORD, JR. 1986. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17: 137-167.
- VOGT, K. A., C. C. GRIER, AND D. J. VOGT. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Adv. Ecol. Res.* 15: 303-377.
- WEERARATNA, C. S. 1979. Pattern of nitrogen release during decomposition of some green manures in a tropical alluvial soil. *Plant Soil* 53: 287-294.
- WIEDER, R., AND G. LANG. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* 63: 1636-1642.
- YAMOAN, C. F., A. A. AGBOOLA, G. F. WILSON, AND K. MULONGOY. 1986. Soil properties as affected by the use of leguminous shrubs for alley cropping with maize. *Agriculture, Ecosystems and Environment* 18: 167-177.