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SHORT COMMUNICATION

Litterfall, decomposition and nutrient release in a lowland tropical rain forest, Morobe Province, Papua New Guinea

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The analysis of litter quantity, litter decomposition and its pattern of nutrient release is important for understanding nutrient cycling in forest ecosystems. Plant growth and maintenance are partly met through nutrient cycling (O'Connell & Sankaran 1997) which is dominated by litter production and decomposition. Litter fall is a major process for transferring nutrients from above-ground vegetation to soils (Vitousek & Sanford 1986), while decomposition of litter releases nutrients (Maclean & Wein 1978). The rate at which nutrients are recycled influences the net primary productivity of a forest. Knowledge of these processes from tropical rain forests is relatively poor (O'Connell & Sankaran 1997), and in particular there are no known published studies on nutrient cycling from lowland tropical forests in Papua New Guinea. The few studies from Papua New Guinea are confined to the mid-montane forest zone (Edwards 1977, Edwards & Grubb 1982, Enright 1979, Lawong *et al.* 1993).

Knowledge of these processes is important for generating ideas about the factors controlling rate of decay. Knowing the factors that control the rate of decay is important since it allows prediction of decay rates for species not studied. Climate and resource quality (e.g. leaf toughness, C/N ratio and N concentration) are considered important factors (Hobbie 1992). Faster decomposition (weight loss) rates are associated with lower C/N ratios (Swift *et al.* 1979) and high initial N concentration (Bosatta & Staaf 1982), while tough

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leaves (resistance to physical damage) decay more slowly than less tough leaves (Sundarapandian & Swamy 1999). Moreover, knowledge of differences in decomposition processes amongst different tree species may be an important aspect for the understanding of tropical forest ecosystem function because of the influence of species composition on the rate and pattern of nutrient release (Hobbie 1992, Torreta & Takeda 1999).

The objectives of this study are to determine patterns of production and disappearance of litter, and nutrient release in a lowland tropical rain forest in Papua New Guinea, and to determine the relative importance of nutrient content and leaf toughness as factors controlling the rate of decay for leaves of the common timber trees: *Pometia pinnata* Forst.f. (Sapindaceae), *Celtis kajewskii* Merrill & Perry (Ulmaceae) and *Dysoxylum caulostachyum* Miq. (Meliaceae).

The study site was located in Morobe Province at Oomsis Forest (6°45′S, 146°47′E), 40 km west of Lae, at *c.* 400 m asl. The forest was selectively logged *c.* 30–35 y ago. Lowland forests in Morobe Province commonly have a basal area of 25–35 m^2 ha^{-1}, but basal areas at Oomsis are *c.* 18 m^2 ha^{-1} (H. M. Rogers, unpubl. data) suggesting the forest had not fully recovered from the logging. This was reflected by the fewer large stems (6) ≥ 50 cm dbh (diameter at breast height). Otherwise the forest appeared little different in structure from unlogged forest, with 426 stems ha^{-1} ≥ 10 cm dbh, a canopy height of 30–35 m, and a well-developed continuous litter layer of 2–4 cm depth. Mean annual rainfall at the nearest weather station (Lae airport, 20 km E, altitude 10 m asl) is *c.* 4800 mm. The mean daily temperature is *c.* 26 °C. The next nearest site for climate at an equivalent altitude to the study site is Hobu (*c.* 40 km NE, altitude 400 m asl), which has a rainfall of 3000 mm evenly distributed throughout the year, and a mean annual temperature of *c.* 26 °C (Rogers & Hartemink 2000). The soils are well drained and derived from schist and are tentatively classified as Chromic Luvisols (Kubo 1992).

Litter was collected in seven litter traps (each 0.7 m × 0.5 m) at 0.8 m above the forest floor, and located at random in a 50-m × 50-m plot. The plot was dominated by *Celtis* spp. (18% of basal area), *Dysoxylum* spp. (6% of basal area) and *Pometia pinnata* (17% of basal area) and comprised at least 51 tree genera (H. Rogers unpubl. data). Litter was collected from each trap every 2 wk for 6 mo (August 1998–February 1999). Litter samples were separated into the three fractions, leaf, reproductive parts, twigs and bark. Each fraction was oven dried at 70 °C and weighed.

The three species, *Pometia pinnata*, *Celtis kajewskii* and *Dysoxylum caulostachyum*, are common commercial species that reach ≥ 50 cm dbh when mature. These species were chosen as they are relatively common and possess leaves that differ in toughness. *Pometia* is considered to have the fastest growth rate of the three species and forms dense uniform stands reflecting fast growth in canopy gaps. Little is known about the other two species. Fresh litter from the three species was collected, oven dried and placed in litter decomposition mesh bags.

Each bag (0.2-m × 0.2-m with a mesh size of 1 mm) contained 20 g of dried litter. Thirty-six litter bags of each of the three species were placed in the forest. Twelve litter bags of each species were placed at three randomly chosen sites within the 50-m × 50-m plot. Using only three sites reduced the possibility of excessive trampling across the plot when retrieving the litter bags. Each litter bag was placed adjacent to bare soil, and covered with litter from the forest floor. Care was taken to avoid any obvious microsite differences when placing the litter bags on the forest floor. All were placed under closed-canopy conditions. At weekly intervals for a period of 12 wk (August–November 1998) three litterbags of each species (one from each site) were removed from the forest and their oven-dried weight determined. Care was taken to remove soil particles and roots from the litter prior to oven drying. Decomposition rate constants (k) were calculated using the first-order exponential equation (Wieder & Lang 1982):

$$L_R/L_I = e^{-kt}$$

Where: L_R = the litter weight remaining at a given time, L_I = the initial weight at time zero, t = the time interval of sampling L_R expressed in years, and k = the decomposition rate constant (y^{-1}). Half-life periods ($t_{0.5}$) were estimated from k using the following equation (Bockheim *et al.* 1991).

$$(t_{0.5}) = \ln(0.5) / (-k) = 0.693 / (-k)$$

Each litterbag was analysed for the following nutrients at the Environmental Analysis Laboratory at Southern Cross University: Organic C, total N, P, K, Mg and Ca. The C/N ratio was also calculated. C and N were analysed by Leco CNS 2000, P by Kjeldahl acid digestion and read colorimetrically using ascorbic acid/ammonium molybdate on a UV/VIS spectrophotometer, and Mg and Ca by nitric acid microwave digest and read by atomic absorption spectrophotometer. A t-test was performed to analyse statistical differences in the nutrient data for individual species over the sampling time, and between species.

Litter fall was variable amongst traps with fruits and flowers showing the greatest variation (Coefficient of variation (CV)= 0.67), followed by twigs (CV = 0.34) and leaf material (CV = 0.39). The high CV for fruit and flowers reflects a single-tree fruiting event adjacent to one of the traps. The litter fall was 5.05 t ha^{-1} based on 6 mo of sampling. Leaf litter made up the largest component, accounting for 86% followed by twigs (11%), and fruit and flowers (3%). The loss in dry weight in litter over the 12 wk varied amongst species. *Dysoxylum* (k = 2.22 y^{-1}, $t_{0.5}$ = 3.7 mo) and *Celtis* (k = 2.12 y^{-1}, $t_{0.5}$ = 4.0 mo) had the highest rates of decay, while *Pometia* (k = 1.17 y^{-1}, $t_{0.5}$ = 5.6 mo) had the lowest. After 12 wk *Dysoxylum* and *Celtis* had 58% and 59% of their initial dry weight remaining, while *Pometia* had 72% remaining. Loss of dry weight was not recorded for longer than 12 wk because the litterbags were becoming contaminated with growth of new roots into the bags, and they were accumulating surface particles of soil that were being washed into the bags during rainfall.

The nutrient concentrations of the fresh leaves were highest in *Dysoxylum* for all nutrients apart from Ca (Table 1). K and Mg showed the greatest decline over 8 wk. Patterns of release of C, N, P and Ca were more variable (Figure 1). Carbon initially showed alternative periods of decline and increase over the first 6–8 wk, but declined overall over 12 wk. N mainly declined over time in *Pometia*, but showed alternate periods of increase and decline in *Celtis* and *Dysoxylum*. For P, levels consistently increased in *Celtis* but mainly declined in *Dysoxylum* and *Pometia*. Ca increased dramatically in *Pometia*, but showed only small fluctuations over time in *Dysoxylum* and *Celtis*. The C/N ratio was lowest in *Dysoxylum* and highest in *Pometia*.

The main component of litter fall by dry weight was leaf material (86%). The annual litter fall of 10.1 t ha^{-1} is within the range of other tropical rain forests (John 1973, Sundarapandian & Swamy 1999, Swift *et al.* 1979), but is higher than the other reported values from Papua New Guinea which are from the lower montane zone. However it is acknowledged that litter fall can be seasonal in tropical forests (Lips & Duivenvoorden 1996), and, since litterfall was measured over 6 mo only, the figure here should be regarded as an estimate. Values from PNG forests include 7.6 t ha^{-1} y^{-1} for a mixed-species lower montane forest at 2400–2500 m asl (Edwards 1977), 7.7 t ha^{-1} y^{-1} from a lower montane *Araucaria hunsteinii* / *Pouteria luzonensis* dominated forest at 950 m asl with *c.* 1600 mm rainfall y^{-1} (Enright 1979), 4.2 t ha^{-1} y^{-1} from a lower montane *Castanopsis accuminatissima*-dominated forest, and 6.3 t ha^{-1} y^{-1} in a lower montane mixed-species forest at 600–1400 m asl with 1512 mm rain y^{-1} (Lawong *et al.* 1993). The higher rate in the lowland Oomsis forest may reflect the higher rainfall and higher mean temperature regime (McAlpine *et al.* 1983) since climate is a primary determinant of litter production (Facelli & Pickett 1991).

The rate of decomposition of litter is strongly influenced by the abiotic environment and resource quality (Swift *et al.* 1979). In the present study the abiotic environment is assumed to be relatively consistent amongst litterbags. However resource quality varied amongst species, which differed in chemical composition and leaf toughness. *Dysoxylum* had the lowest C/N ratio and highest initial % N (2.73%) and decomposed at the highest rate ($k = 2.22$), while *Pometia* had the highest C/N ratio, intermediate initial % N (1.80%), and decomposed at the slowest rate. Although the rates of decay (k) are consistent with other tropical studies (Swift *et al.* 1979), they may be underestimates due to the 1-mm mesh size of the litter bags which could exclude soil macrofauna from the litter.

The three species also differed in the physical toughness of their leaves (resistance to physical damage) which can also affect the rate of decomposition. Tough leaves are generally resistant to decomposition (Sundarapandian & Swamy 1999). Leaves of *Dysoxylum* were least tough, while *Pometia* leaves were most tough with particularly strong midribs. In addition, dry leaves of *Dysoxylum* broke easily and could be crushed to fine particles with ease. *Pometia* leaves

Table 1. Nutrient concentration (%) of fresh leaves and after 12 wk.

Sampling time	Species	C	N	C/N	P	K	Ca	Mg
0 wk	*Pometia*	(a) 43.7 a	(a) 1.80 a	(a) 24.3 a	(a) 0.14 a	(a) 0.49 a	(a) 1.37 a	(a) 0.34 a
	Celtis	(b) 32.9 a	(b) 1.50 a	(b) 21.9 a	(b) 0.07 a	(b) 0.93 a	(b) 5.33 a	(a) 0.33 a
	Dysoxylum	(a) 44.1 a	(c) 2.73 a	(c) 16.1 a	(c) 0.16 a	(b) 1.05 a	(c) 1.71 a	(b) 0.39 a
12 wk	*Pometia*	(a) 39.2 a	(a) 1.56 b	(a) 25.2 a	(a) 0.09 b	(a,b) 0.29 b	(a,b) 2.96 a	(a) 0.24 b
	Celtis	(b) 27.9 a	(a) 1.65 a	(b) 16.9 b	(a) 0.09 a	(a) 0.32 b	(a) 4.82 a	(a) 0.21 a
	Dysoxylum	(a,c) 36.1 a	(a) 2.77 a	(b) 13.0 a	(a) 0.11 b	(b) 0.23 b	(b) 1.85 a	(a) 0.24 b

For each species different letters in parentheses indicate significant differences between species for each sampling time ($P \leq 0.05$). Significant differences over time for individual nutrients are indicated by letters not in parentheses ($P \leq 0.05$).

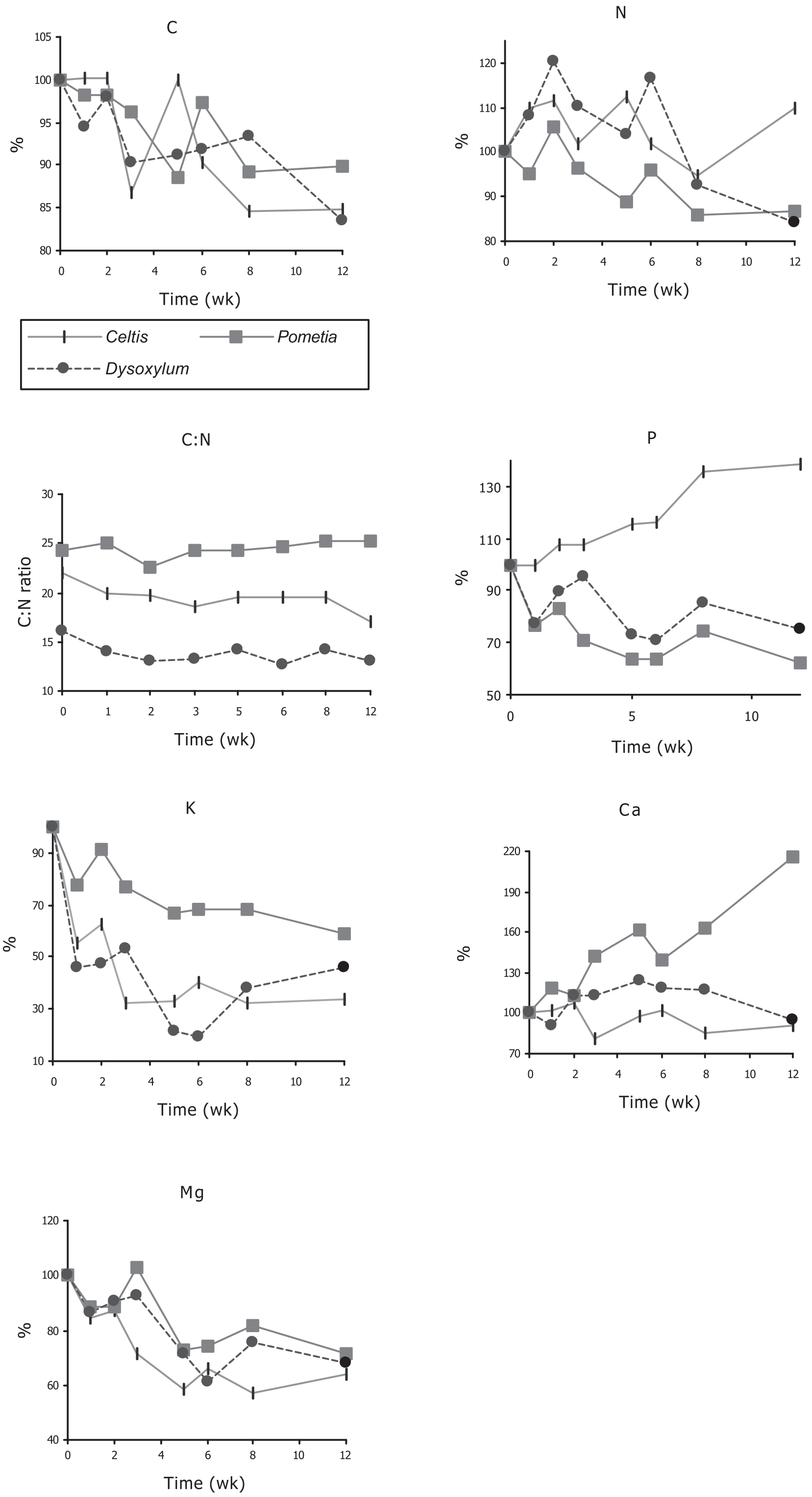

Figure 1. Percentage of initial mass remaining over time (wk) from leaf litter of *Pometia pinnata*, *Celtis kajewskii* and *Dysoxylum caulostachyum*.

were more difficult to break, and when crushed broke into larger particles. The size of a particle determines the ability of a decomposer organism to ingest the material. Smaller particles also provide an increased surface area of substrate to act as a stimulus to the microbial population (Swift *et al.* 1979).

The general pattern of nutrient release from decomposing leaves in tropical forests involves (1) an initial phase when leaching and nutrient release predominate; (2) a net immobilization phase during which nutrients are imported into the residues by microbes; and (3) a net release phase when the nutrient mass decreases (Swift *et al.* 1979). However N and P dynamics can vary from this model, being characterized by early immobilization (net accumulation) and followed by net release (Vitousek & Sanford 1986). This occurred in *Celtis* for P and *Dysoxylum* and *Celtis* for N only. Patterns of nutrient release for the other elements are generally consistent with other studies. Potassium was the most mobile, declining rapidly over the measurement period, reflecting that it is readily leached (O'Connell & Sankaran 1997).

Carbon and nitrogen dynamics are related to the relative availability of C and N to the microbial population. In many decomposition studies nitrogen mobilization commences at the critical C/N ratio of about 20–30 in temperate forests and 30–40 in tropical forests (Torreta & Takeda 1999). In this study C/N ratios were more similar to temperate forest values. However there did not appear to be a critical value at which nitrogen mobilization commenced in any one of the species. Nitrogen mobilization was most consistent and generally most rapid in *Pometia* which had the highest and most consistent C/N of *c.* 25 over the 12 wk. This is contrary to what might be expected for a species with a low C/N where N may be limiting to the decomposer community. An accumulation of N would seem more likely.

All three species displayed alternate periods of immobilization and release to some extent, particularly in *Dysoxylum* and *Pometia*, reflecting periods when N was plentiful and then limiting to the decomposition process. Phosphorus showed mainly release in *Dysoxylum* and *Pometia* in contrast to *Celtis*, which indicated net immobilization. *Celtis* had the lowest initial P (0.07%), therefore P may need to be imported by microbes for effective litter decomposition.

In conclusion, patterns of litterfall, decomposition and nutrient release in this study are generally comparable to studies in tropical forests from other regions. However, there was no distinct indication of the influence of nutrients in the decay of the three species. It may be that nutrients played almost no role in the control of litter decay in the present study. Although the C/N ratio may have a role in determining the rate of decay, the fact that *Pometia* lost N at the fastest rate while decomposing at the slowest rate presents a confusing picture. It can also be inferred that climate was not a significant influence either, since if it was the primary controlling factor rates of decay would be identical for all three species. The most important factor related to rate of decay appeared to be leaf toughness, with *Pometia* leaves having the greatest resistance to physical damage and *Dysoxylum* the least.

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LITERATURE CITED

BOCKHEIM, J. G., JEPSEN, E. A. & HEISEY, D. M. 1991. Nutrient dynamics in decomposing leaf litter of four tree species on a sandy soil in northwestern Wisconsin. *Canadian Journal of Forest Research* 21:803–812.

BOSATTA, E. & STAAF, H. 1982. The control of nitrogen turn-over in forest litter. *Oikos* 39:143–151.

EDWARDS, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea II. The production and disappearance of litter. *Journal of Ecology* 65:971–992.

EDWARDS, P. J. & GRUBB, P. J. 1982. Studies of mineral cycling in a montane rain forest in New Guinea. *Journal of Ecology* 70:649–666.

ENRIGHT, N. J. 1979. Litter production and nutrient partitioning in rainforest near Bulolo, Papua New Guinea. *The Malaysian Forester* 42:202–207.

FACELLI, J. M. & PICKETT, S. T. A. 1991. Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 57:1–32.

HOBBIE, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 17:336–339.

JOHN, M. D. 1973. Accumulation and decay of litter and net production of forest in West Africa. *Oikos* 24:431–435.

KUBO, T. 1992. *A study on the forest soils of Papua New Guinea, Preliminary reports of short term experts attached to JICA projects and their counterparts for the period 1980–1990*. Kristen Press, Lae. 131 pp.

LAWONG, B., POULI, T. & ANTON, G. W. 1993. Rates of litter decomposition in different habitats in Bulolo area, Morobe Province. Pp. 161–166 in Höft, R (ed.). *Proceedings of the Biological Society of New Guinea*, Wau Ecology Institute, Wau.

LIPS, J. M. & DUIVENVOORDEN, J. F. 1996. Fine litter input to terrestrial humus forms in Colombia Amazonia. *Oecologia* 108:138–150.

MACLEAN, D. A. & WEIN, R. W. 1978. Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. *Canadian Journal of Botany* 56:2730–2749.

McALPINE, J. R., KEIG, G. & FALLS, R. 1983. *Climatic tables for Papua New Guinea*. Australian National University Press, Canberra.

O'CONNELL, A. M. & SANKARAN, K. V. 1997. Organic matter decomposition and mineralisation. Pp. 443–480 in Nambiar, E. K. S. & Brown, A. G. (eds). *Management of soil, nutrients and water in tropical plantation forests*. ACIAR, Canberra.

ROGERS, H. M. & HARTEMINK, A. E. 2000. Soil seed bank and growth rates of an invasive species, *Piper aduncum*, in the lowlands of Papua New Guinea. *Journal of Tropical Ecology* 16:243–251.

SUNDARAPANDIAN, S. M. & SWAMY, P. S. 1999. Litter production and leaf-litter decomposition of selected tree species in tropical forests at Koydyar in the Western Ghats, India. *Forest Ecology and Management* 123:231–244.

SWIFT, M. J., HEAL, O. W. & ANDERSON, J. W. 1979. *Decomposition in terrestrial ecosystems*. Blackwell Scientific, Oxford. 372 pp.

TORRETA, N. K. & TAKEDA, H. 1999. Carbon and nitrogen dynamics of decomposing leaf litter in a tropical hill evergreen forest. *European Journal of Soil Biology* 35:57–63.

VITOUSEK, P. M. & SANFORD, R. L. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17:137–167.

WIEDER, R. & LANG, G. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* 63:1636–1642.