Mass and Nutrient Dynamics of Decaying Litter from Passiflora mollissima and Selected Native Species in a Hawaiian Montane Rain Forest

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Mass and nutrient dynamics of decaying litter from *Passiflora mollissima* and selected native species in a Hawaiian montane rain forest

PAUL G. SCOWCROFT

Institute of Pacific Islands Forestry, USDA Forest Service, Pacific Southwest Research Station, 1151 Punchbowl St., Rm. 323, Honolulu, HI 96813, U.S.A.

ABSTRACT. The structure and functioning of *Acacia koa-Metrosideros polymorpha* forests between 1200 and 1800 m elevation on the island of Hawaii are being threatened by *Passiflora mollissima*, an aggressive introduced liana from South America. This study was done to evaluate the short-term decomposition dynamics of *Passiflora* and selected native leaf and twig litter. The nutrient-rich, non-sclerophyllous *Passiflora* leaves completely disappeared in less than 5 mo. The estimated time for native leaf litter to lose 95% of initial dry weight ranged from 1.65 y for N-rich *Acacia* phyllodes to 6.67 y for *Cibotium glaucum*; for woody litter, the time ranged from 4.5 y for *Acacia* twigs to 23 y for *Acacia* bark. Except for *Cibotium* frond litter, decay rates were significantly correlated with initial lignin-ash ratios. *Passiflora* litter did not accelerate decomposition of *Acacia* and *Metrosideros* leaf litter. *Passiflora*, *Acacia*, and *Metrosideros* leaf litter showed net mineralization of N, P, Ca, K, and Mg during the study. *Cibotium* frond litter showed significant accumulation of N, Ca, and Mg; P levels stayed constant and K was rapidly lost. In general, twigs experienced a net loss of most nutrients, while bark experienced either no change or a significant net gain of nutrients. Nutrient cycling has increased in *P. mollissima* infested forests.

KEY WORDS: *Acacia koa*, *Cibotium glaucum*, decomposition, Hawaii, litter quality, *Metrosideros polymorpha*, nutrient cycling, *Passiflora mollissima*

INTRODUCTION

Biological invasions of the native tropical rain forests of Hawaii can occur unnoticed until well advanced, and a threat to remnant native ecosystems. Successful invaders often displace natives by creating shade so dense that native plants can not survive, and by occupying safe sites for establishment of native seedlings (Vitousek *et al.* 1987). But the effects of invading species may not always be obvious. Vitousek & Walker (1989) concluded that *Myrica faya* Aiton (faya tree), an introduced nitrogen-fixer was changing ecosystem level characteristics of young volcanic sites on the island of Hawaii, including nitrogen cycling processes. Exploratory work in 1985 (Scowcroft 1986) suggested that *Passiflora mollissima* (Kunth) L.H. Bailey (banana poka), an introduced vine, may be altering rates of nutrient cycling in montane rain forests.

Passiflora mollissima is native to the Andes Mountains where it grows between 2000 and 3600 m elevation (Escobar 1980). The vine is uncommon in its native

habitat and it is not a forest pest because native insects intensively feed on it (Gilbert 1975). It was first observed in Hawaii in 1921 (La Rosa 1984). By 1981 heavy infestations were reported on about 710 km^2 on the islands of Kauai and Hawaii in wet and mesic forests (Warschauer *et al.* 1983).

Passiflora vines are capable of rapid growth in the high light environment of natural and man-made forest gaps, where it can quickly smother natural regeneration, shrubs, ferns, and understorey trees (Scowcroft & Nelson 1976, Warschauer *et al.* 1983). The vine is capable of climbing 20 m into the crowns of older overstorey trees, forming a curtain to the forest floor (La Rosa 1984), which increases wind breakage and wind throw.

Preliminary study of litterfall in young *Acacia koa* A. Gray (koa) stands developing after logging indicated that *Passiflora* litter can make up more than 10% of the total fine litterfall and over 25% of the leaf litterfall (Scowcroft 1986), which was within the range of values reported for lianas in other tropical rain forests (Hegarty 1991, Hladik 1974). More importantly, in these young post-logging stands of nitrogen-fixing *Acacia*, *Passiflora* litter accounted for more than 30% of the nitrogen, phosphorus, and calcium returned to the forest floor (Scowcroft 1986). Thus, nutrient return seemed to have increased as a result of *Passiflora* establishment.

If decomposition were also greater in *Passiflora*-infested forests, then increased nutrient availability might enable *Passiflora* and other rapid-growing, nutrient-demanding introduced species to become even more competitive (Gerrish & Mueller-Dombois 1980, Vitousek & Walker 1989). Furthermore, increased soil nutrient availability could result in production of more decomposable, higher quality litter due to a 'self-reinforcing feedback loop within the intrasystem nutrient cycle' (Perry 1994: 410–411).

Litter quality, which is that set of intrinsic chemical and structural characteristics that govern activity of decomposer organisms, and hence the ease with which organic matter decays (Swift *et al.* 1979), is particularly important in the tropics. Lavelle *et al.* (1993) described a hierarchical model of decomposition for terrestrial ecosystems, in which climate (more specifically moisture and temperature) normally exerts the greatest control on decomposition. Soil characteristics are usually the next most important controlling factor, followed in order by litter quality, macroorganisms, and microorganisms. But in the tropics, where climatic and edaphic factors generally favour decomposition, litter quality exerts the greatest control (Lavelle *et al.* 1993, Meentemeyer 1978).

Lignin concentration is a widely used index of litter quality. It is highly resistant to decomposition, and has been shown to exert a controlling influence over plant decomposition, both in temperate (Fogel & Cromack 1977, White *et al.* 1988) and tropical ecosystems (Laishram & Yadava 1988, Tian *et al.* 1992). Other commonly used indices include initial tissue nitrogen and phosphorus concentration, lignin to nitrogen concentration, and various carbon to nutrient ratios (Aber *et al.* 1990, Constantinides & Fownes 1994, Melillo *et al.* 1982, Swift *et al.* 1979, Taylor *et al.* 1989a). Thaiutsa & Granger (1979) concluded that

decomposition should be most rapid for litter containing large amounts of ash and nitrogen, but small amounts of lignin and polyphenolics, and low C : N ratio.

Because litter quality strongly influences decomposition, Seastedt (1984) and Chapman *et al.* (1988) hypothesized that mixing high quality, rapidly decaying litter with low quality, more slowly decaying litter should affect decay rates and nutrient dynamics. However, results of the few studies that have tested this hypothesis have been inconclusive (Blair *et al.* 1990, Taylor *et al.* 1989b).

Litter quality, especially carbon : nutrient ratios, also affects nutrient dynamics of decomposing litter (Perry 1994). Generally, microbial decomposers are presented with an oversupply of carbon in forest litter relative to their needs, but an insufficient supply of one or more nutrients. The usual outcome is immobilization of those nutrients that are in short supply during initial stages of decomposition, followed by mineralization of those same elements once carbon:nutrient ratios of the partially decomposed material have narrowed sufficiently to relieve the nutrient limitation.

One objective of this study was to compare the decay rates and nutrient dynamics of *Passiflora* and native foliage, singly and in mixture. It was hypothesized that litter quality would be a major factor controlling decomposition and nutrient dynamics, and that the non-sclerophyllous, nutrient-rich leaves of *Passiflora* would decay fastest, followed in order by nitrogen-rich *Acacia* phyllodes, sclerophyllous *Metrosideros polymorpha* Gaud. (ohia) leaves, and lastly by *Cibotium glaucum* (Smith) H. & A. (tree fern) foliage. It was also hypothesized that mixing *Passiflora* litter with the native litters would stimulate decomposition of the latter. Finally, it was hypothesized that the more recalcitrant native litter would immobilize nutrients, especially nitrogen and phosphorus, during initial stages of decomposition, but *Passiflora* would not. The other objective was to compare decay rates and nutrient dynamics of fine woody litter (twigs and bark) of *Acacia* and *Metrosideros*.

STUDY AREA

This study was conducted in the tropical montane rain forest of the Laupahoehoe section of the Hilo Forest Reserve located at about 1400 m elevation on the windward slopes of Mauna Kea, island of Hawaii. Daily temperatures average 14°C and annual rainfall averages 3200 mm (Giambelluca *et al.* 1986) with less rain falling during summer months.

Soil in the study area formed in volcanic ash over fragmental a'a (scoriaceous) lava, and was classified as Alic Fulvudands (Soil Survey Staff 1994), which had 50 to 85% aluminum saturation, a water content at 15000 kPa tension of 12% or more, less than 35% (by volume) rock fragments and a mean annual soil temperature of 8 °C to 15 °C. Its pH ranged from extremely acid (4.0 pH) at the surface to medium acid (6.0 pH) at 50 cm depth. Nitrogen and phosphorus fertility were relatively high (Crews *et al.* 1995).

The vegetation in the study area was a native mixed-species forest. The open to closed canopy overstorey consisted of emergent *Metrosideros* and *Acacia* 30 m in height. Common woody understorey species include *Cibotium*, *Cheirodendron trigynum* (Gaud.) A. Heller (olapa), *Coprosma rhynchocarpa* A. Gray (pilo), *Myrsine lessertiana* A. DC (kolea), *Rubus hawaiiensis* A. Gray (akala) and *Vaccinium calycinum* Sm (ohelo). Like many tree species in other tropical montane rain forests (e.g. Mooney *et al.* 1984), *Acacia*, *Metrosideros*, and *Cibotium* foliage exhibit a high degree of sclerophylly. *Passiflora* was the most structurally-dominant of the introduced species.

METHODS

Field studies

The litter bag method was used to study decomposition dynamics. Bags were *c.* 18 cm × 20 cm and constructed of fibre glass screen with a mesh size of 1.5 mm. Preliminary investigation showed that earthworms, millipedes, and other small litter feeding invertebrates had ready access to bag contents.

A randomized complete block design with five replicates was used to study decomposition of 12 types of litter:

Pure leaf litter	Mixed leaf litter	Woody litter
Acacia	*Acacia-Metrosideros*	*Acacia* twigs (<5 mm dia.)
Metrosideros	*Acacia-Passiflora*	*Acacia* bark
Passiflora	*Metrosideros-Passiflora*	*Metrosideros* twigs (<5 mm dia.)
Cibotium	*Acacia-Metrosideros-Passiflora*	*Metrosideros* bark

Freshly fallen *Acacia*, *Metrosideros*, and *Passiflora* leaf litter were collected from the forest floor. Most of the *Metrosideros* leaf litter was non-senescent leaves blown down by strong winds. Senescent fronds were collected from standing live *Cibotium*. *Metrosideros* and *Acacia* twigs and bark were collected from recent blow-down trees. All materials were collected during a 5-wk period, February and early March 1987; and enough litter was collected in a given week to satisfy the needs of one complete replicate. Collections were taken to the laboratory where they were air-dried for at least 2 wk to bring them to a relatively uniform moisture content. As collections were made, fresh foliar litter subsamples were drawn at random and their specific leaf areas were determined. Leaf areas were measured using a LiCOR portable leaf area meter (model LI3000A).

After air-drying, *c.* 15 g of material were placed in each bag. When two or three types of litter were mixed in a bag, the amounts of each type were determined by their proportion in natural litterfall (i.e., *Acacia-Metrosideros*, 1:3 by weight; *Acacia-Passiflora*, 3:1; *Metrosideros-Passiflora*, 9:1; *Acacia-Metrosideros-Passiflora*, 3:9:1) (Scowcroft 1986). Subsamples of each type of litter were taken during the filling to get correction factors for converting initial air-dry weights

to oven-dry weights. A second set of subsamples was taken to determine lignin, ash, and nutrient concentrations. A third set were soaked for 24 h in deionized water to evaluate potential loss of dry weight and nutrients through leaching.

On 3 April 1987 filled and labelled bags were randomly distributed over the forest floor within five replicate pig-proof exclosures, which ranged in size from 1000 m^2 to 2000 m^2. The exclosures were necessary to prevent feral pigs from destroying the bags. The only constraint on bag placement was that each bag had to lie on the forest floor. There was no appreciable litter layer covering the soil such as exists in temperate forests, so bags lay on mineral soil. Each exclosure contained a complete replicate set of bags.

Bags were retrieved at 28, 56, 84, 140 and 252 d after emplacement. Four bags per litter type were collected each time from each replicate exclosure. Although the content of each bag was oven-dried and weighed separately, the four samples were bulked for chemical analyses. Decayed material in mixed-litter bags was not separated by species.

Three supplementary experiments were installed at the same time as the main experiment. The first used tethered *Acacia* and *Metrosideros* leaves to determine whether the mesh bags affected rates of decomposition. The second used bags containing only 3 g of air-dried *Passiflora* and *Cibotium* litter per bag to determine whether the relative heavy loading of 15 g air-dry material per bag in the main experiment affected rates of decomposition. Both of these supplementary experiments ran for 252 d, and they were installed in only one exclosure. The third experiment used bags loaded with mixed leaf litter in equal proportions by weight to determine if loading ratio affected decomposition rates of native leaf litter in mixed bags. Bags for this experiment were retrieved after 140 d.

Rainfall was measured during the study in a bulk rain gauge, read every 7–10 d; and air temperature was recorded on a hygrothermograph.

Chemical analyses

Retrieved samples were sorted to remove insects, dried (70 °C), weighed, and ground in a Wiley mill. Chemical analyses were made at the University of Hawaii Agricultural Diagnostic Center. Ash content (muffle furnace at 525 °C, 4 h) was determined on subsamples to convert weight remaining to ash-free dry weight basis (AOAC 1980). Total nitrogen content was determined by Kjeldahl digestion and analysis by colorimetric methods (Issac & Johnson 1976, Shuman *et al.* 1973). Organic carbon was determined by chromatic acid digestion and spectrophotometric methods (Heanes 1984). Lignin concentration was measured by the sequential system of Goering & Van Soest (1970).

Subsamples used for mineral analyses were dry-ashed (Isaac & Johnson 1985). Potassium concentrations were determined by Technicon continuous-flow flame-emission spectrophotometry. Phosphorus, calcium and magnesium were determined by inductively-coupled plasma emission spectrometry (Perkin Elmer ICP model 6500).

Statistical analysis

Separate multivariate and univariate repeated measures analyses of variance (Freund *et al.* 1986, Khattree & Naik 1995, SAS Institute 1985) were used to examine differences in dry weight and nutrient dynamics among foliar litter types and among woody litter types over the course of the study. Each repeated measures analysis of variance was done with an autoregressive error structure using the PROC MIXED procedure (SAS Institute 1992). A simpler error structure called *compound symmetry* did not appear to be adequate using the output from the multivariate repeated measures approach of the PROC GLM procedure. Litter types within replicates were the subjects repeatedly measured over time; exposure time and type × time interaction were within subject effects. Multiple pairwise comparisons were done using ouput of PROC MIXED to evaluate differences among litter types within a measurement time and among measurement times within a litter type; probability levels for individual paired tests were adjusted to give an overall $\alpha \leq 0.05$.

The exponential decay regression model (Wieder & Lang 1982) was fitted to the decomposition data for each litter type using the SAS procedure NLIN (SAS Institute 1985). Untransformed data were used for all regressions. The first order decomposition model was $W/W_o = e^{-kt}$, where W is the dry weight remaining at time t, W_o is the initial dry weight, and k is the rate constant. The length of time (y) for 95% of the initial litter weight to be lost was estimated as $3/k$ (Olson 1963).

The effect of initial litter quality was evaluated by examining correlations between initial dry weight remaining and (a) initial concentrations of lignin, N, P, and total ash, and (b) initial ratios of lignin:N, lignin:P, and lignin:ash. Analyses were done using the combined foliar-woody data set because foliage, twigs, and bark were fine litter whose decomposition was assumed to be mainly a function of litter quality rather than massiveness. Untransformed and, where warranted, log transformed data for the independent variables were used.

To determine whether the nutrient–rich, non-sclerophyllous *Passiflora* leaves speeded decay of *Metrosideros* or *Acacia* leaves, expected percentage weight loss values were calculated for mixed-litter bags assuming that weight loss was a function of decay rates for component species and the amount of each initially put in the bags. Expected values (E_t) were calculated as follows:

$$E_t(\%) = \left(\Sigma_{i=1}^{3} W_i \cdot f_{it} \;/\; \Sigma_{i=1}^{3} W_i \right) \cdot 100$$

where W_i is the initial ash-free dry weight of species i that was weighed into a mixed-species bag, and f_{it} is the fraction of initial weight remaining at time t for species i in a single-species bag. Exponential decay regressions were then fitted to the expected values.

RESULTS

Weather

Weather conditions during the study were generally favourable for decomposition. Maximum day time temperatures ranged from about 10 to 23 °C, and throughout much of the study were above 14 °C (Figure 1a). Lowest temperatures were usually associated with rainfall events. Rainfall occurred every week during the study. The least amounts recorded were during August (days 210 to 244) when rainfall averaged only 4 mm wk^{-1} (Figure 1b). The fourth collection (day 233) was made during this period. In all, 2350 mm of rain was recorded during this study.

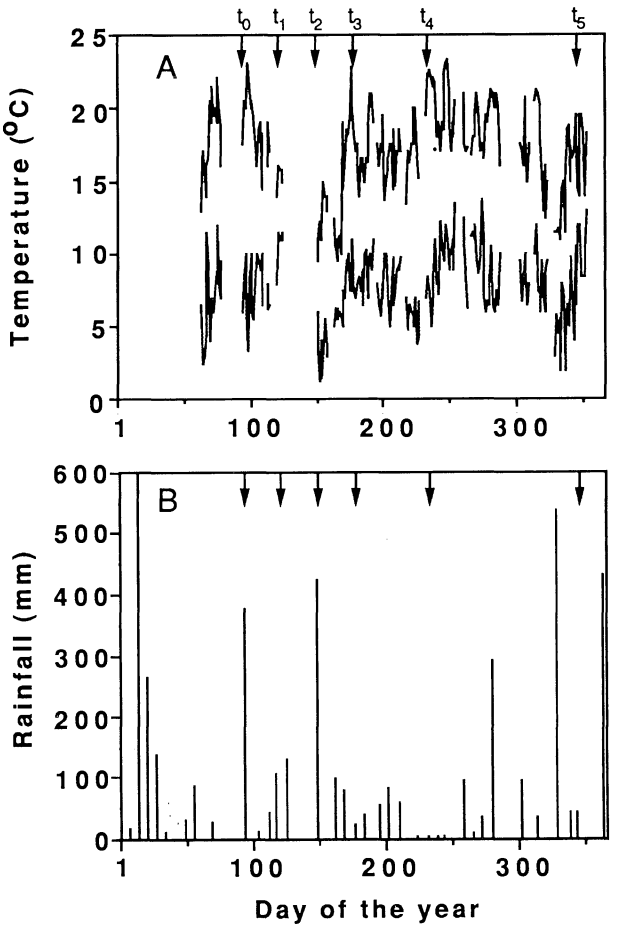

Figure 1. Patterns of (a) maximum and minimum temperatures and (b) rainfall during the study period (3 April to 8 December 1987) at 1400-m elevation in the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii. Gaps in temperature traces denote instrument failure. Rainfall bars show total rainfall collected in a bulk precipitation gauge during the 7-14 d period prior to the date of plotting. Arrows show the Julian day when the study started (t_0 = day 93) and when bags were retrieved (t_1 = day 121, t_2 = day 149, t_3 = day 177, t_4 = day 233, and t_5 = day 345).

Foliar litter decay rates

Repeated measures analysis of variance for foliar litter indicated that there were significant differences in decay rates among litter types. *Passiflora* litter decomposed significantly faster than the other foliar litter types (Figure 2a). Virtually all of it was gone by day 140. *Acacia* was the next most rapidly decaying litter with about 27% of the initial dry weight remaining at the end of the study. Nearly 40% of the dry weight of *Metrosideros* litter was still present at 252 d. However, differences in decay of *Acacia* and *Metrosideros* leaf litter during the course of this study were not statistically significant. Decomposition of *Cibotium* was significantly slower than the other foliar litters. About 75% of the initial ash-free dry weight was still present after 252 d (Figure 2a) and most pinnae were intact.

Decomposition of leaf litter followed the first-order exponential decay patterns observed in a preliminary study (Scowcroft 1986). Decay constants (k) for *Passiflora*, *Acacia*, *Metrosideros*, and *Cibotium* leaf litter were 8.05, 1.82, 1.39, and 0.45, respectively (Table 1). The corresponding times for loss of 95% of initial weight were 0.4, 1.6, 2.2, and 6.7 y. The decay curve for *Cibotium* approximated a straight line (zero order decay curve).

Laboratory tests indicated that for *Cibotium* leaching of water-soluble organic

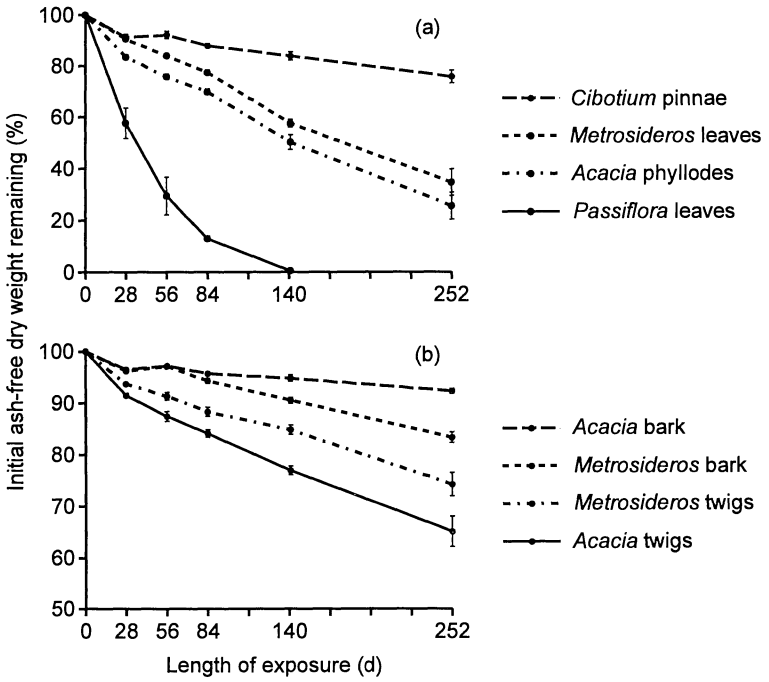

Figure 2. Observed loss of initial ash-free dry weight of (a) foliar and (b) woody litter during 252 d of decomposition in the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii. Error bars are ±1 SE (n = 5 for each plotted point).

Table 1. First order exponential decay constants (k) and estimated length of time (T_{95}) for 95% loss of initial ash-free dry weight of foliar and woody litter (n = 5 for each mean). The 95% confidence limits for each mean are in parentheses.

Type of litter	Decay constant	T_{95} weight loss (y)
Foliar litter		
Passiflora	8.05	0.37
	(6.91–9.20)	(0.33–0.43)
Acacia	1.82	1.65
	(1.66–1.98)	(1.51–1.81)
Metrosideros	1.39	2.16
	(1.26–1.52)	(1.97–2.38)
Cibotium	0.45	6.67
	(0.38–0.51)	(5.88–7.89)
Woody litter		
Acacia twigs	0.67	4.48
	(0.61–0.73)	(4.11–4.92)
Metrosideros twigs	0.46	6.52
	(0.41–0.50)	(6.00–7.32)
Metrosideros bark	0.26	11.54
	(0.24–0.28)	(10.71–12.50)
Acacia bark	0.13	23.08
	(0.11–0.15)	(20.00–27.27)

matter could have accounted for the initial loss of ash-free weight observed during the first month of decomposition in the field. This was not true for *Passiflora*, nor for *Acacia* and *Metrosideros* leaf and twig litter; they lost significantly more ash-free weight in the field than could be attributed to leaching (Table 2).

Results (not shown) of supplementary tests of bag and bag loading effects showed: (1) that confinement in mesh bags did not significantly affect decomposition of *Acacia* and *Metrosideros* leaf litter; and (2) that relatively heavy loading (*c.* 15 g air-dry weight) of mesh bags did not significantly affect decomposition of *Passiflora* or *Cibotium* foliage.

Woody litter decay rates

Twigs and bark decomposed relatively slowly. Estimated time for loss of 95% of initial weight ranged from 4.5 y ($k = 0.67$) for *Acacia* twigs to 23.1 y ($k = 0.13$)

Table 2. Mean (and SE) loss of ash-free dry weight (%) of leaves and twigs of *Passiflora* and native litter after 28 d in the field and after 24 h of leaching in the laboratory (n = 5 for each mean). Comparisons between actual field and laboratory leaching loss made by paired t-tests.

Type of litter	Field weight loss	Laboratory leaching loss	P(t)
Foliar litter			
Passiflora	42.4 (6.0)	18.8 (0.9)	0.02
Acacia	16.5 (1.0)	6.2 (0.4)	<0.01
Metrosideros	9.0 (0.4)	2.5 (0.4)	<0.01
Cibotium	8.8 (1.3)	8.2 (0.8)	0.37
Woody litter			
Acacia twigs	8.5 (0.4)	0.7 (0.2)	<0.01
Metrosideros twigs	6.3 (0.3)	0.9 (0.3)	<0.01

for *Acacia* bark (Table 1). As with *Cibotium*, the first-order exponential decay curves were not significantly different from the zero order decay curves. Wieder & Lang (1982) noted that litter with small proportions of readily leachable and labile compounds appear to follow a linear decay rate, at least for the first two years.

Decomposition of *Acacia* and *Metrosideros* twigs did not differ significantly until after day 56; then *Acacia* showed the more rapid decay. By the end of the study, *Acacia* twigs had lost *c.* 35% of their initial ash-free weight; *Metrosideros* twigs had lost *c.* 25% (Figure 2b). The difference in weight loss may have been partly due to invertebrate preference for decomposing *Acacia* twig bark; invertebrate grazing was obvious and extensive on *Acacia* twigs, but less so on *Metrosideros* twigs. Laboratory leaching losses of ash-free dry weight were very small for *Acacia* and *Metrosideros* twigs (Table 2). Leaching of water soluble material from twigs appeared to be a minor component of ash-free dry weight losses during the first month in the field.

Acacia and *Metrosideros* bark decomposed at statistically similar rates through the first 140 d of exposure (Figure 2b). However, by the end of the study the thick dense *Acacia* bark had lost only 8% of its initial ash-free weight (not statistically significant), whereas the thin flaky *Metrosideros* bark had lost *c.* 17% (significant). Both types of bark decayed significantly slower than either type of twig.

Litter quality relationships

Lignin concentrations ranged from *c.* 170 to 200 g kg^{-1} for leaf litter, and from *c.* 220 to 380 g kg^{-1} for woody litter (Table 3). Differences in lignin concentrations among the foliar litter types were not statistically significant. The ash concentrations of *Passiflora* and *Cibotium* leaf litter were more than twice as large as those of *Acacia* and *Metrosideros* leaf litter (Table 3). Although *Acacia* and *Metrosideros* twigs and *Metrosideros* bark had ash concentrations similar to *Acacia* and *Metrosideros* leaves, *Acacia* bark had a very low ash concentration.

Structurally, *Passiflora* leaves were thinner and less sclerophyllous than the other foliar litters. Not only was specific leaf area at least three times larger for *Passiflora* than for the other species, *Passiflora* lost up to seven times more dry weight through leaching in laboratory tests (Table 3). About 75% of the loss was due to leaching of soluble organic matter. The initial carbon:nitrogen ratio of *Passiflora* and *Acacia* leaves was about 20 while that of *Metrosideros* and *Cibotium* foliage was greater than 35 (Table 3). Despite similar C : N ratios, *Cibotium* decomposed much more slowly than *Metrosideros* leaves.

As indicated by high ash concentration, *Passiflora* leaf litter was nutrient rich (Figure 3). Nitrogen concentration in *Passiflora* was nearly equal to that in *Acacia* litter, and was about twice as great as that in *Metrosideros* and *Cibotium* litter. Concentration of phosphorus was 2.5 times greater in *Passiflora* leaves than in the other types of leaf litter. Calcium and magnesium concentrations were also much higher in *Passiflora*.

Table 3. Mean (and SE from ANOVA) carbon, lignin, and ash concentration, C : N ratio, specific leaf area, and dry weight loss during 24 h leaching in the laboratory for undecomposed *Passiflora* and native litter (n = 5 for each mean). Values for foliar or woody litter in a given column that share a common letter are not significantly different ($\alpha \leq 0.05$, Bonferroni pairwise multiple comparison procedure).

	Concentration (g kg^{-1})			C:N	Specific leaf area	Dry weight loss on leaching (%)	
Species	Carbon	Lignin	Ash	Ratio	(cm^2 g^{-1})	Total	Due to soluble OM
Foliar litter							
Passiflora	467a	171a	110b	20.9a	183.7a	22.1a	75.6b
Acacia	449a	169a	47a	22.9a	50.9b	7.3b	80.5ab
Metrosideros	429a	197a	43a	38.8b	65.5b	3.2c	73.0b
Cibotium	458a	195a	105b	35.4b	58.7b	8.8b	89.0a
(SE)	(10)	(8)	(4)	(1.4)	(7.9)	(0.6)	(2.4)
Woody litter							
Acacia twigs	442ab	226a	34ab	32.7a	n.a.	2.0a	80.8a
Metrosideros twigs	445ab	262b	42b	59.3b	n.a.	1.5a	53.4a
Acacia bark	413a	283b	18a	26.9a	n.a.	missing	missing
Metrosideros bark	457b	380c	44b	118.0c	n.a.	missing	missing
(SE)	(8)	(6)	(5)	(3.4)		(0.4)	(11.3)

n.a. = not applicable

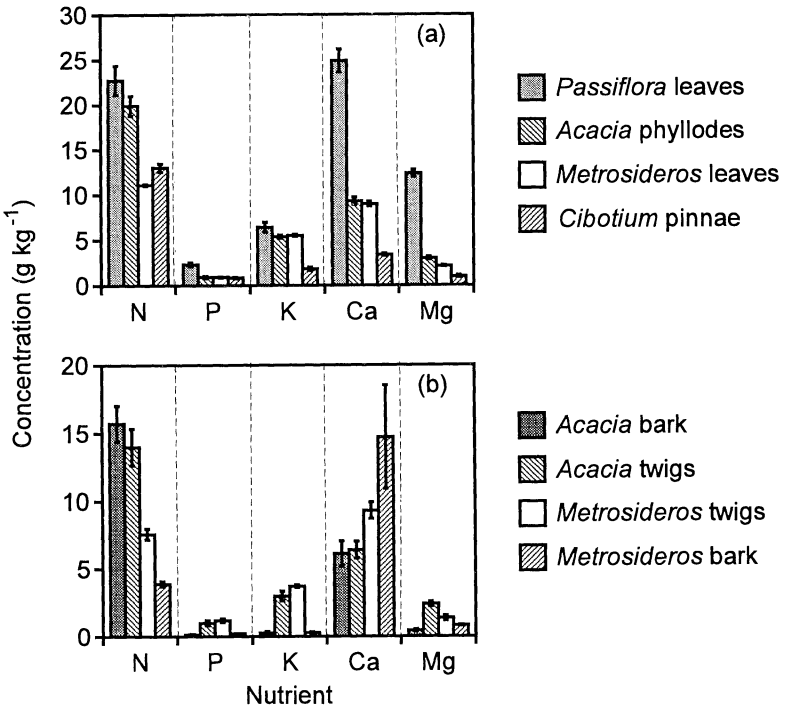

Figure 3. Mean (±1 SE) concentrations of major nutrients in undecomposed (a) foliar litter of *Passiflora mollissima*, *Acacia koa*, *Metrosideros polymorpha*, and *Cibotium glaucum*, and (b) fine twigs and bark litter of *A. koa* and *M. polymorpha* from the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii (n = 5 for each mean).

Table 4. Coefficients of determination and significance level for correlations between percent initial ash-free mass remaining after 252 d of decomposition and each of seven different litter quality indices. The effect of including or excluding foliar tree fern data in the correlations is also shown.

Index	Including fern	Excluding fern
N	0.473	0.492
P	0.617*	0.633*
Ash	0.227	0.639*
Ln(lignin)	0.615*	0.786**
Ln(lignin : N)	0.469	0.551
Ln(lignin : P)	0.597*	0.699*
Ln(lignin : ash)	0.482	0.916*

* $P \leq 0.05$, ** $P \leq 0.01$

Several litter quality indices were significantly correlated with decomposition (Table 4). Initial phosphorus concentration, *ln* initial lignin concentration, and *ln* lignin : P each explained about 60% of the variation in weight remaining after 252 d of exposure. These correlations improved when *Cibotium* data were excluded; the improvement was greatest for *ln* lignin. But the best correlation was obtained using *ln* lignin : ash as the index of litter quality and excluding the *Cibotium* data (Figure 4).

The effect of Passiflora *on native litter decomposition*

Passiflora leaf litter did not accelerate decay of native leaf litter when mixed in proportions found in natural litterfall (Figure 5). Only in two instances did decay of mixed litter even come close to being significantly greater than expected. After 56 d, the *Acacia-Passiflora* mixture had 59.4% initial ash-free weight remaining compared with 64.8% expected ($P = 0.055$). After 84 d, the *Metrosideros-Passiflora* mixture had 68.7% remaining compared with 71.3% expected ($P = 0.051$).

Differences between observed and expected amounts of mixed litter left after 140 d were affected by the mixing ratio. In the third supplementary experiment, the 1 : 1 *Acacia-Passiflora* mixture lost significantly more dry weight than expected (Table 5). The 1 : 1 : 1 *Acacia-Metrosideros-Passiflora* mixture lost only marginally more dry weight than expected, whereas the natural-loading mixture clearly did not lose more than expected.

Foliar litter nutrient dynamics

Analysis of the nutrient dynamics of foliar litter revealed several general patterns (Figure 6). First, species-specific losses of nutrients tended to parallel the species-specific losses in ash-free dry weight, K being the notable exception (cf. Figure 2a). Second, *Acacia* and *Metrosideros* leaf litter lost carbon and nutrients at rates that were not significantly different. Potassium was an exception with initial loss from *Acacia* leaf litter exceeding that from *Metrosideros* litter. Third, *Cibotium* was the only leaf litter that showed significant net accumulation of nutrients, specifically nitrogen, calcium and magnesium. Fourth, at any

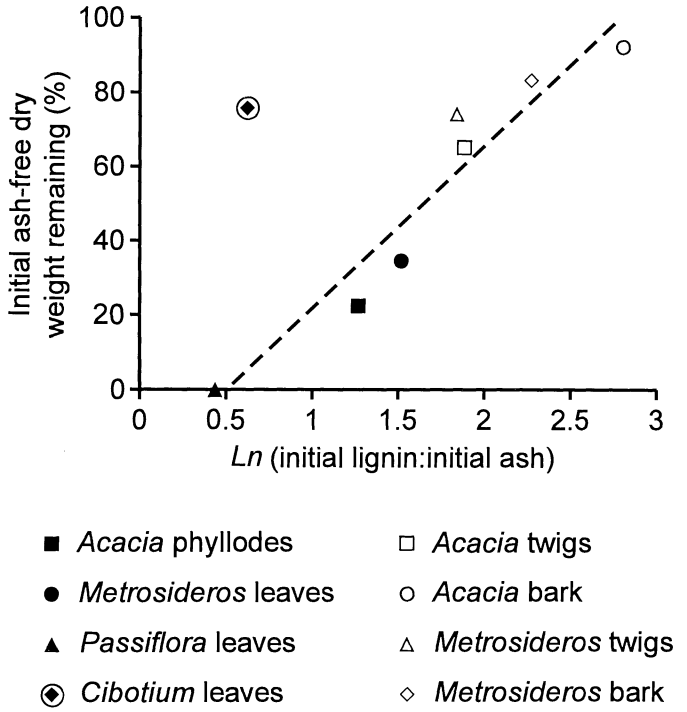

Figure 4. Relationship between the natural log of the ratio of initial lignin concentration to initial ash concentration (an index of litter quality) and the percentage ash-free dry weight remaining after 252 d decomposition. The least squares fit [owt = $-22.0 + 43.7ln$(lignin : ash), $r^2 = 0.92$] excludes the *Cibotium glaucum* datum.

given time, the magnitude of nutrient losses for the four types of foliar litter followed the general pattern, *Passiflora*>*Acacia* = *Metrosideros*>*Cibotium*. And finally, the relative ranking of nutrients based on the amount of loss from foliar litter showed the following order: K>P = Mg>Ca>N. However, analysis detected significant differences in the percentages lost only between K and each of the other nutrients.

Woody litter nutrient dynamics

Nutrient dynamics of twigs and bark (Figure 7) were more complex than those of foliar litter, making it difficult to generalize. The loss of carbon from woody litter proceeded more slowly than loss of initial dry weight (cf. Figure 2b). After 252 d, *Acacia* and *Metrosideros* twigs had lost significant amounts of C, but there was no statistical evidence that either type of bark had lost or gained C. In contrast to carbon, phosphorus was lost from twigs more rapidly than ash-free twig weight (cf. Figure 2b). *Acacia* and *Metrosideros* twigs showed similar patterns of nutrient losses and gains, except for Ca, which was present in large amounts in *Acacia* twigs by the end of the study. Net nutrient accumulations

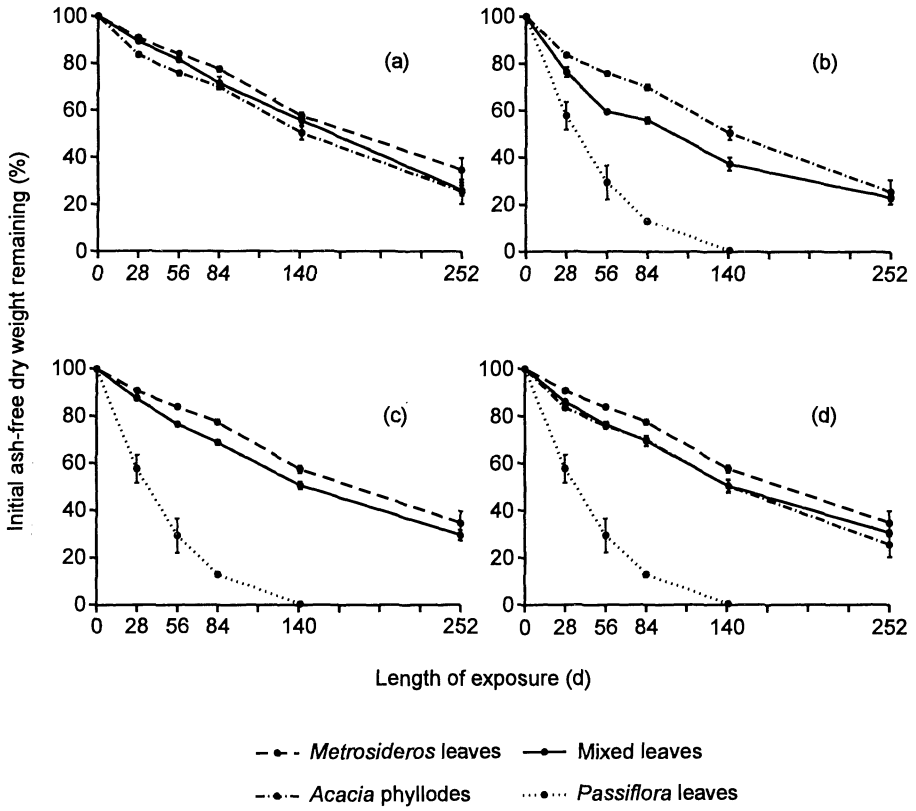

Figure 5. Losses of initial ash-free dry weight (%) for mixed leaf litter of (a) *Acacia koa-Passiflora mollissima*, (b) *A. koa-Metrosideros polymorpha*, (c) *M. polymorpha-P. mollissima*, and (d) *A. koa-M. polymorpha-P. mollissima* compared to losses for unmixed component litters during 252 d of decomposition in the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii. Error bars are ±1 SE (n = 5 for each plotted point).

Table 5. Mean (and SE) observed and expected percentage of ash-free dry weight remaining after 140 d for mixed-leaf-litter bags loaded with equal amounts of the component species and with loadings according to proportions found in natural litterfall (given in parentheses below each litter type). Comparisons between observed and expected means made by paired t-test (n = 5 for each mean).

Litter type (Ratio in litterfall, by weight)	Uniform loading ratio			Natural loading ratio		
	Observed (%)	Expected (%)	P(t)	Observed (%)	Expected (%)	P(t)
Acacia-Metrosideros	52.3	53.8	0.61	55.5	55.7	0.91
(1 : 3)	(2.8)	(1.3)		(2.0)	(1.0)	
Acacia-Passiflora	22.0	26.2	0.03	37.2	38.4	0.31
(3 : 1)	(1.3)	(1.5)		(2.8)	(2.2)	
Metrosideros-Passiflora	27.7	29.9	0.66	50.7	52.1	0.54
(9 : 1)	(4.3)	(0.8)		(1.6)	(1.3)	
Acacia-Metrosideros-Passiflora	32.1	36.8	0.06	50.3	51.6	0.65
(3 : 9 : 1)	(1.6)	(0.9)		(2.5)	(1.0)	

generally occurred in bark litter. *Metrosideros* bark accumulated nitrogen, phosphorus, and potassium; the apparent net accumulation of magnesium (Figure 7) was not statistically significant. Similarly, *Acacia* bark showed net gains of phosphorus, potassium, calcium, and magnesium during the study. Finally, the relative magnitude of nutrient loss for the four types of woody litter followed the general pattern, *Acacia* twigs = *Metrosideros* twigs > *Metrosideros* bark = *Acacia* bark.

DISCUSSION

The results supported the hypothesis that structural and chemical composition of litter is correlated with decomposition rates; indeed, the non-sclerophyllous, nutrient-rich leaves of *Passiflora* disappeared at least three times faster than the more sclerophyllous native leaf litters. However, there is little in the tissue chemistry data to indicate why *Cibotium* fronds decomposed so much slower than the three other leaf types. Loss of weight was not well correlated with any of the litter quality indices examined. Lignin concentrations, which were intermediate to the ranges reported for other tropical montane forests (La Caro & Rudd 1985, Laishram & Yadava 1988, Vitousek *et al.* 1994), were not significantly different among the four types of leaf litter. Nutrient dynamics of decaying *Cibotium* was also different from the other types of leaf litter. Apparently factors other than those measured here were inhibiting decomposition of *Cibotium*, perhaps concentrations of polyphenolics.

Except for *Passiflora*, decay constants for leaf litter in the present study were generally within the ranges (0.5 to 2.3) reported for other tropical montane forest species (Lisanework & Michelsen 1994, Tanner 1981; Thompson & Vitousek, in press, Vitousek *et al.* 1994, Wiegert 1970). Crews *et al.* (1995) found that k was 0.82 for *Metrosideros* leaf litter decaying at a slightly lower elevation site (1170 m) in Laupahoehoe. The higher rate constant for *Metrosideros* leaves in the present study ($k = 1.39$) was probably due to the non-senescent nature of the litter, which consisted mainly of blow-down leaves that contained higher concentrations of N, P, and K than normally found in senescent foliage (Balakrishnan & Mueller-Dombois 1983, Crews *et al.* 1995; Vitousek *et al.* 1988, 1994, 1995.

Crews *et al.* (1995) hypothesized that nutrient availability and circulation may be increased on fertile sites through a positive feedback created by the production of nutrient-rich, readily-decomposable litter that rapidly releases its nutrients. If true, then introducing a species like *Passiflora* whose litter is more nutrient-rich and more decomposable than the native litters could accentuate the positive feedback, and further increase availability and nutrient cycling. Native plants may benefit, but there is a possibility that invasive introduced species would benefit even more (Gerrish & Mueller-Dombois 1980, Vitousek & Walker 1989).

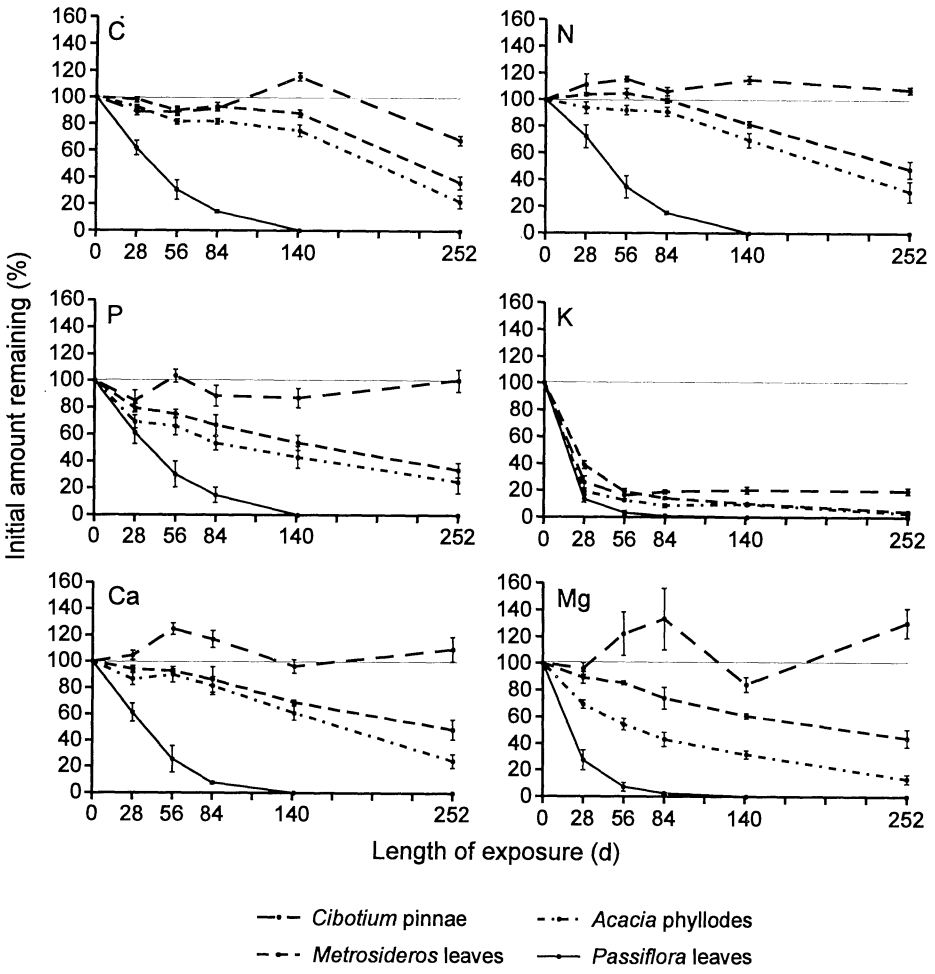

Figure 6. Mean (±1 SE) amount of carbon and nutrient elements (N, P, K, Ca, Mg) remaining as a percentage of the initial amount in foliar litter of *Passiflora mollissima*, *Acacia koa*, *Metrosideros polymorpha*, and *Cibotium glaucum* over a 252-d period in the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii (n = 5 for each plotted point). Horizontal reference lines denote 100% initial amount remaining.

Mixing *Passiflora* with native leaf litter did not affect decomposition of the latter. The lack of a synergistic effect in mixed species litter decomposition has been reported for temperate hardwoods and conifers (Blair *et al.* 1990, Klemmedson 1992, Staaf 1980, Thomas 1968), and may be the rule rather than the exception.

Environmental factors (e.g. soil nutrient availability) strongly influences litter quality (Perry 1994). There is evidence that some montane tropical forests are deficient in both nitrogen and phosphorus relative to lowland tropical forests (Gerrish *et al.* 1988; Tanner *et al.* 1990, 1992; Vitousek *et al.* 1993). The prevailing hypothesis states that litter produced under such nutrient limitations will be of poor quality and slow to decompose, and will initially immobilize

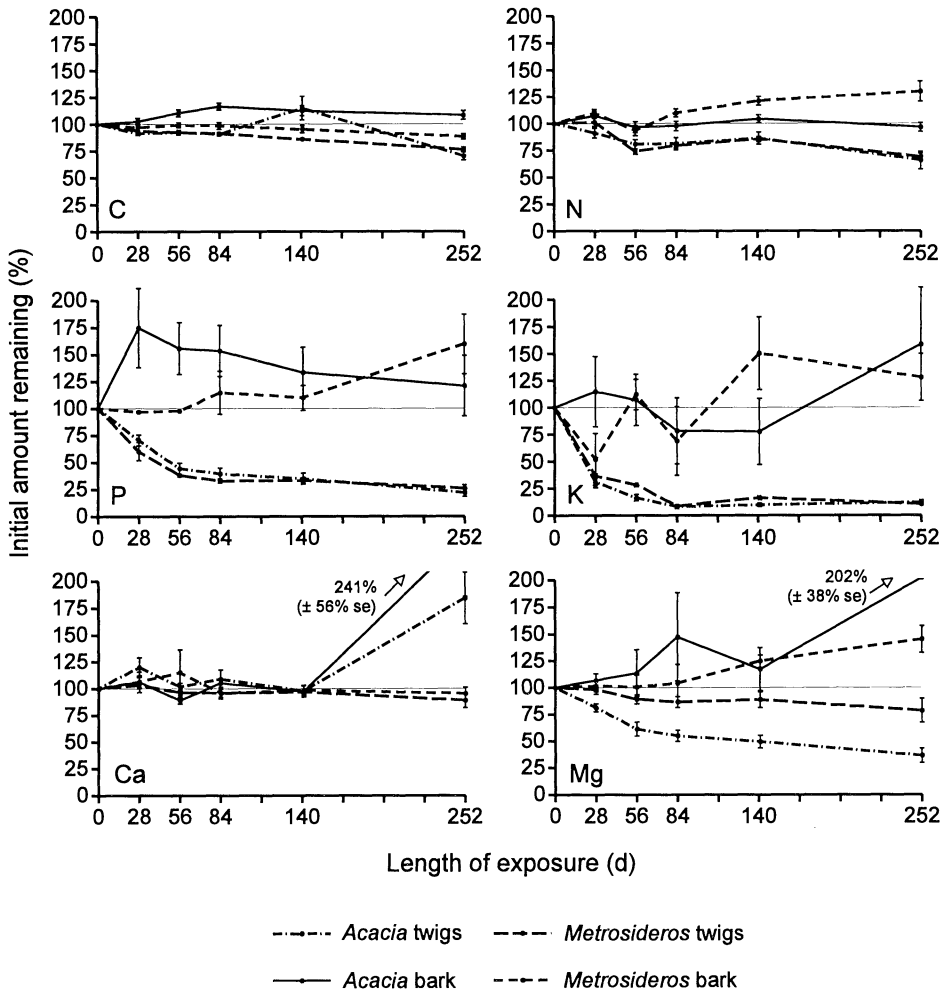

Figure 7. Mean (±1 SE) amount of carbon and nutrient elements (N, P, K, Ca, Mg) remaining as a percentage of the initial amount in *Acacia koa* and *Metrosideros polymorpha* twig and bark litter over a 252-d period in the Laupahoehoe section of the Hilo Forest Reserve, Island of Hawaii (n = 5 for each plotted point). Horizontal reference lines denote 100% initial amount remaining.

those elements in short supply (Chapin *et al.* 1986, Vitousek 1982). If true, litter nutrient concentrations and decay dynamics may be used as indices of site fertility. The general lack of immobilization in the current study indicated that the nutrient supply was high relative to demand. Crews *et al.* (1995) found that nitrogen and phosphorus availability was high at sites where net mineralization occurred in decaying *Metrosideros* litter, but low at sites where net immobilization occurred. It appears that across the range of sites used by Crews *et al.* (1995) and in this study, decay dynamics were good indices of site fertility.

In conclusion, the data indicated that nutrient turnover in this Hawaiian forest has increased due to the the presence of the alien, *Passiflora*. Whether

the potential benefit to native species of increased nutrient turnover outweighs the potential harm of increased competition and structural damage remains unanswered. There seems little doubt that *Passiflora* has become an integral part of the ecosystem.

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