

LEAF HERBIVORY AND DECOMPOSABILITY IN A MALAYSIAN TROPICAL RAIN FOREST

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Abstract. There is accumulating evidence that similar suites of plant traits may affect leaf palatability and leaf litter decomposability. However, the possible association between leaf herbivory and litter decomposition rates across species in species-diverse natural ecosystems such as tropical rain forests remains unexplored, despite its importance in estimating the herbivory effects on carbon and nutrient cycling of ecosystems. We found no strong association between leaf herbivory and litter decomposition rates across 40 tree species in a Malaysian tropical rain forest, even though the leaf and litter traits were tightly correlated. This is because the leaf and litter traits related to herbivory and decomposition rates in the field were inconsistent. Leaf toughness accounted for only a small part of the variation in the herbivory rate, whereas a number of litter traits (the leaf mass per area, lignin to nitrogen ratio, and condensed tannin concentration) accurately predicted the decomposition rate across species. These results suggest that herbivory rate across species may not be strongly related to single leaf traits, probably because plant–herbivore interactions in tropical rain forests are highly diverse; on the other hand, plant–decomposer interactions are less specific and can be governed by litter chemicals. We also investigated two factors, phylogeny and tree functional types, that could affect the relationship between herbivory and decomposition across species. Phylogenetic relatedness among the species did not affect the relationship between herbivory and decomposition. In contrast, when the plants were segregated according to their leaf emergence pattern, we found a significant positive relationship between herbivory and decomposition rates for continuous-leaving species. In these species, the condensed tannin to N ratios in leaves and litter were related to herbivory and decomposition rates, respectively. However, we did not observe a similar trend for synchronous-leaving species. These results suggest that the relationship between herbivory and decomposition may be more greatly affected by functional types than by phylogenetic relatedness among species. In conclusion, our results suggest that well-defended leaves are not necessarily less decomposable litter in a tropical rain forest community, implying that herbivory may not generate positive feedback for carbon and nutrient cycling in this type of ecosystem.

Key words: condensed tannins; decomposition; herbivory; leaf emergence pattern; leaf traits; lignin; litter traits; LMA; nitrogen; phylogenetically independent contrast; total phenolics; tropical rain forest.

INTRODUCTION

In terrestrial ecosystems, the above- and belowground subsystems are closely related through the carbon (C) and nutrient cycles, and plant species traits play a key role in enforcing the feedback between them (Hobbie 1992, Wardle 2002). Moreover, foliar herbivores can have a variety of effects on this feedback by altering the quantity and quality of resources that plants provide to decomposers (Bardgett et al. 1998), although the extent of these effects is ecosystem specific (Bardgett and Wardle 2003). In forest ecosystems, usually <10% of the foliage is consumed by herbivores because the leaves of

forest plant species are often well defended (Hairton et al. 1960); consequently, the vast majority of the leaves produced in a given year enter the soil subsystem as plant litter (Hairton and Hairton 1993). This litter serves as a major source of organic C and nutrients for soil organisms (Berg and McClaugherty 2003). Thus, the plant traits selected through such aboveground interactions as herbivory can potentially affect the belowground subsystems by influencing litter quality (Grime et al. 1996, Wardle et al. 1998, Cornelissen et al. 1999).

It has been suggested that the litter produced by more heavily defended plant species is more recalcitrant for decomposers than that produced by less heavily defended species (Grime et al. 1996). This is because foliar defensive traits, such as total phenolics, condensed tannins, lignin, physical toughness, and the leaf mass per area (LMA) (Bryant et al. 1987, Wainhouse et al. 1990, Shimada and Saitoh 2003) also reduce decomposer performance (Melillo et al. 1982, Horner et al. 1988,

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Gallardo and Merino 1993, Cornelissen 1996, Kraus et al. 2003). Evidence for this association has emerged from studies of leaf palatability to invertebrates or digestibility in rumen extracts performed alongside litter decomposition bioassays for the same plant species (Grime et al. 1996, Wardle et al. 1998, Cornelissen et al. 1999, 2004). The positive relationship between palatability or digestibility and decomposability implies that herbivory has the ecological or evolutionary potential to control such processes as C and nutrient cycling. Assuming that there is a strong positive association between herbivory and decomposition in natural ecosystems, herbivore-induced changes in the plant community could generate positive feedback for C and nutrient cycling (Hobbie 1992). However, the palatability or digestibility of a given plant species for generalist herbivores in the laboratory depends on the herbivore species used for testing, although the results of such feeding tests may provide a rough measure of a plant's susceptibility to herbivory in the field (Perez-Harguindeguy et al. 2003). In the field, several species of herbivores usually coexist in a single ecosystem and specialized plant-herbivore relationships are common. It is therefore plausible that in nature a different association exists between herbivory and decomposition at the community level than would be expected from the relationship between palatability and decomposability predicted by a feeding experiment. All of the available herbivores and decomposers in a given area exert selective pressure on plant traits; thus, it is important to investigate the rates of herbivory and decomposition at the community level under natural conditions.

In the present study, we focused on the relationship between foliar herbivory and litter decomposability across a range of plant species in a highly diverse tropical rain forest ecosystem. No previous study has examined the relationship between litter decomposability and foliar herbivory across plant species in a natural forest ecosystem, with the exception of that by Wardle et al. (2002). They reported a significant positive relationship between litter decomposability and changes of vegetation density in response to browsing mammals (deer and goats) for 59 understory and 18 canopy tree species in a natural forest in New Zealand, implying that herbivorous mammals have a large effect on the feedback with C and nutrient cycling in that system. However, herbivory in tropical rain forests is quantitatively and qualitatively different from that in the temperate zone (Coley and Barone 1996). The high level of tree species diversity in tropical rain forests results in considerable variation in leaf traits. Furthermore, insect herbivores cause most of the damage observed on leaves and have selected for a wide variety of plant chemical, developmental, and phenological defenses. Insect herbivores typically have a narrow host range in the tropics, and damage by specialist herbivores is generally greater than that caused by generalist herbivores (Barone 1998). However, little is known about the relative pressures

from specialist and generalist herbivores in tropical rain forests (Coley 1983). Thus, it is difficult to predict the damage level in the field from laboratory results. Moreover, the plant species considered in earlier studies belonged to several groups (e.g., ferns, herbs, graminoids, and woody species); thus, the significant relationship between herbivory and decomposition was largely driven by differences between plant groups. In fact, the same relationship is not necessarily detectable within groups (Grime et al. 1996, Wardle et al. 1998, 2002, Cornelissen et al. 2004). In tropical rain forests, however, most aboveground production involves just one group of plants: angiosperm trees. Therefore, it is necessary to investigate the relationship between herbivory in the canopy and decomposition of tree communities to predict the effects of herbivory on ecosystem processes. These features of tropical rain forests may reveal a different relationship between herbivory and decomposition than was previously observed in the system of Wardle et al. (2002).

We also investigated two factors that could potentially affect the relationships between herbivory and decomposition across tree species. First, phylogenetic constraints among plant species related to plant-herbivore interactions (Novotny et al. 2002) or chemical production (Villar et al. 2006) may affect the relationship between herbivory and decomposition. Second, responses to herbivory may be specific to tree functional types (e.g., evergreen vs. deciduous), and these differential responses may cause differences in litter quality (Chapman et al. 2006). We used leaf emergence patterns to define tree functional types. Leaf emergence patterns are generally related to leaf longevity, photosynthetic rate, and individual growth rate; species with continuous leafing tend to have shorter leaf life spans, higher photosynthetic rates, and higher plant growth rates relative to species with synchronous leafing, and these properties are related to particular leaf traits, e.g., LMA and foliar nitrogen (N) (Kikuzawa 1983, Reich et al. 1992). Furthermore, these leaf emergence patterns are also suggested as components of the defensive traits of plants (Kursar and Coley 2003). For example, synchronous leafing is one strategy used by species to satiate specialist herbivores (Aide 1993). Clearly, leaf emergence patterns may affect the relationship between herbivory and decomposition rates. Thus, we explored the relationship between herbivory and decomposition in consideration of the phylogenetic relatedness among plant species and plant types by segregating species according to their leaf emergence patterns.

The tropical rain forests of Borneo, Malaysia, have high sympatric tree diversity (~1200 tree species/52 ha; Wills et al. 2006); thus, they provide an excellent opportunity to elucidate the effects of both environmental and phylogenetic factors on the target phenomena. Here, we utilized canopy access facilities that enabled us to collect living leaf samples and observe herbivory in the tree canopy layer (50–60 m). We

focused on the following questions. (1) Is there a significant positive relationship between the leaf herbivory rate and the litter decomposition rate across species? (2) Does phylogeny or a difference in the leaf emergence pattern among species influence these relationships? To answer these questions, we examined the relationships between living leaf (hereafter, leaf) and leaf litter (hereafter, litter) traits and determined which traits were related to leaf herbivory and litter decomposition across a diverse range of tropical tree species.

MATERIALS AND METHODS

Study site and species selection

The study was conducted in primary forests in Lambir Hills National Park (LHNP), 4°12' N, 114°02' E, 150–250 m a.s.l. (above sea level), and in neighboring secondary forests developed after shifting cultivation in Sarawak, Malaysia. All study sites were located within 4 km of each other. The primary forests show extreme richness in plant species diversity (Wills et al. 2006) and are dominated by dipterocarp trees in the canopy and emergent layers (Ashton 1991). The average annual precipitation for 2000–2003 was 2428 mm. The daily mean temperature in the canopy layer is nearly constant throughout the year (about 26°C; daily range 23–32°C). The soils are nutrient-poor sandy or clay soils (Yamakura et al. 1995). In the study forests, most leaf damage was caused by insect herbivores. Due to recent human influences, mammalian herbivores, such as monkeys, are rare. At LHNP, there is a canopy observation system (walkway and ladders) at the center of the Canopy Biology Plot (CBP; 8 ha) and a canopy crane (80 m tall with a 75 m long jib) at the center of the Crane Plot (CP; 4 ha), located about 500 m northeast of the CBP.

Previously, we measured several leaf traits (concentrations of total phenolics, condensed tannins, lignin, C, N, and LMA) for about 250 tree species belonging to 48 families present in the region including the Lambir area and the Ulu Baram area (2°50' N, 114°50' E, 150–600 m a.s.l.), which is ~150 km away (H. Kurokawa et al., *unpublished manuscript*). We selected 40 tree species from primary forests in LHNP and neighboring secondary forests that encompassed the range of leaf traits observed in the 250 tree species, as determined using principal component analyses. Thus, our study was conducted in a relatively small area (within 4 km) compared to previous studies (Cornelissen et al. 1999, Wardle et al. 2002), but the selected species were representative of those present in the larger area (150 km). Furthermore, the selected species belonged to eight families not closely related to each other in the phylogenetic tree of the 48 families present in the region (Appendices A and B).

Sample collection and trait measurement

Leaves and litter were collected from one to three trees for each of the 40 species in the CBP, CP, and neighboring secondary forests. Mature sun leaves were

collected from three positions in the canopy layer for each sampled tree (about 60 leaves for each tree) using a canopy crane, a walkway system, and a ladder, in June 2002. Fresh leaf litter that had fallen within the previous three days was collected from the forest floor beneath each sampled tree between August 2002 and January 2003 (~100–200 g in dry mass for each species). The leaf and litter samples were pooled separately for each individual tree. For each leaf and litter sample, subsamples were taken for measurements of toughness and LMA. Additional subsamples were vacuum freeze-dried for 16 h and then powdered in a vibrating sample mill (model TI-100; CMT, Kyoto, Japan) for chemical analysis. The rest of the litter samples were oven-dried (40°C to constant mass) and pooled by species in loosely tied polyethylene bags and stored in a drying room until the decomposition trial.

The toughness (originally measured as kilogram-force; values multiplied by 98.0665 to get SI units of kPa) of the leaves and litter was determined by the mass needed to penetrate a leaf using a column 3 mm in diameter (Nomura et al. 2000). Three measures were performed for each of five leaves and litter samples per tree and then averaged for each tree. The LMA (mg/cm^2) was measured for each of 20 leaves and 20 litter samples and then averaged for each tree. A proanthocyanidin assay was used to determine the condensed tannin content with cyanidin chloride, a commercially available anthocyanidin, as a standard curve (Julkunen-Titto 1985). The Folin-Ciocalteu method was used to determine the total phenolic content (Waterman and Mole 1994) using tannic acid as a standard curve. An improved acetyl bromide procedure (Iiyama and Wallis 1990) was used to determine the lignin content. The concentration of lignin was calculated to fit the equation derived from Fukushima and Hatfield (2001). The concentrations of C and N in the leaves were analyzed using an NC analyzer (SUMI-GRAPH NC-900; Sumitomo Chemical, Osaka, Japan). Standard curves were prepared using hippuric acid. All leaf and litter traits were measured for each sampled tree and then averaged for each species.

From April 2003 to May 2005, new leaf production and the loss of leaves were assessed every six months, or every three months for those species with the high leaf turnover rate, for each of 10 branches per sampled tree (one to three trees per species; same trees as for sample collection) by marking the leaves with a pen. The leaf life span for each tree was calculated using the equation of King (1994) and was averaged for each species.

Herbivory rate

It has been proposed that in the tropics nearly 70% of a leaf's lifetime damage due to herbivory occurs while it is expanding (Coley and Barone 1996, Kursar and Coley 2003). We also observed that reductions in leaf area due to herbivory rarely occurred on fully expanded, mature leaves. Consequently, we assumed that the reduction in

area for each mature leaf was roughly equal to the accumulated damage over its entire lifetime. Damage to mature leaves was assessed in the canopy four times between April 2003 and May 2005. At each observation, 50–100 leaves were randomly selected from each tree (one to three trees per species; the same trees as for sample collection). If there was evidence of a leaf being eaten, we measured the percentage loss in area for each leaf by comparing the damaged leaf area to the area of the inferred intact leaf shape using the scanned images of them. The amount lost from individual leaves through herbivory was averaged for each tree. The accumulated damage to each tree was determined as the average of the measurements taken on the four dates. This measurement had the potential to underestimate the damage, because completely removed leaves were not included. Southwood et al. (1986) suggested that damage per unit of time exposed could be obtained by dividing the accumulated damage by the life span of the leaf, because foliage palatability and the rate of damage by herbivory are inversely correlated with leaf life span (Coley 1983). Therefore, we adopted the following equation to estimate the herbivory rate for each tree:

$$Y = \ln(hX + 1)$$

where Y is the accumulated damage, h is the herbivory rate, and X is the leaf life span. The herbivory rates were then averaged for each species.

Decomposition rate

Decomposition rates were estimated using a litterbag method. Each litter sample was oven-dried to a constant mass at 40°C before the trial, and about 5 g (dry mass) of each species' litter were enclosed in a 2-mm mesh nylon cloth litterbag (20 × 20 cm). Depending on the amount of litter collected, 15–28 bags were prepared for each species. These bags were placed on the soil surface within a plot (14 × 5 m) established on a flat area next to the CBP at LHNP on February 2003. After 3, 6, 12, and 24 weeks, five to seven bags per species were collected from the plot, and soil or other plant tissue on the remaining litter was carefully removed with a brush. The reduction in dry mass was determined after drying the samples to a constant mass at 40°C, and mean values of mass loss were calculated for each sampling time for each species. The decomposition rate was calculated for each species using Olson's k (Olson 1963) according to the following equation:

$$W_t = W_0 \exp(-kt)$$

where W_t is the litter mass after a given period, W_0 is the initial mass, and t is the time in years.

Data analyses

First, we examined interspecific variation in the leaves and litter for each of the following traits: total phenolics, condensed tannins, lignin, and N content per unit leaf area and per unit leaf mass, LMA, and toughness. The

chemical compositions were compared per unit area to identify changes in the amount of each chemical through senescence and per unit mass to investigate changes in collective leaf and litter quality. At the interspecies level, the relationships among traits for both leaf and litter and the relationships between the leaf or litter traits and the rate of herbivory or decomposition were evaluated by correlation analyses. In addition, stepwise multiple regression analysis was applied to the same traits as those used in the correlation analyses to determine which combinations of leaf and litter traits served as the best predictors of interspecific variation in herbivory and decomposition rates. The relationship between the rates of herbivory and decomposition was examined by simple linear regression analysis.

The relationships among the leaf and litter traits and between those traits and the rate of herbivory or decomposition were also analyzed in an evolutionary context using phylogenetically independent contrasts (PICs; Garland et al. 1992), which do not depend on the assumption that species represent statistically independent data points. First, we constructed a hypothesis for the phylogenetic relationship among the studied species using the program Phylomatic, a phylogenetic database and tree assembly tool kit (*available online*).⁴ We used the maximally resolved tree, based on a recent interpretation (Angiosperm Phylogeny, version 5; Stevens 2004) of the Angiosperm Phylogeny Group, APG II (2003) phylogenetic classification of angiosperm plant orders and families, as the backbone of our phylogenetic hypothesis. The tree produced by Phylomatic was well resolved at the family level but placed the genera as polytomies within families and species as polytomies within genera. We calculated PICs for all pairs of leaf and litter traits, between the leaf or litter traits and herbivory or decomposition rates, and between the herbivory and decomposition rates using COMPARE, an online program for the statistical analysis of comparative data (*available online*).⁵ We assumed that all branch lengths were equal when conducting our PIC analyses, a method that has been shown to provide a proper Type I error rate in comparative analyses when true branch lengths are uncertain or unavailable (Ackerly 2000).

The degree of synchrony in the leaf emergence patterns for each tree was calculated as the coefficient of variation (CV) for the ratio of the number of new leaves to the total number of leaves marked previously at four sampling times throughout the monitoring period (Coley 1983). A high value indicates a close degree of synchrony, whereas a low value indicates more continuous production of young leaves over the observation period. We also assigned the plant species to two types depending on their leaf emergence patterns:

⁴ (<http://www.phylodiversity.net/phylomatic/phylomatic.html>)

⁵ (<http://compare.bio.indiana.edu>)

those species with $CV < 0.9$ were classified as having a relatively continuous leaf emergence pattern and those with $CV \geq 0.9$ as having a relatively synchronous leaf emergence pattern; 0.9 was selected, because the median of the CVs across all of the species was 0.903 (Appendix B). The CV was not available for *Myristica gigantea*, *Madhuca carassipes*, *Glochidion glomerulatum*, and *Tarenna cumingiana* (Appendix B); however, *Myristica gigantea* and *Madhuca carassipes* were categorized as having synchronous leaf emergence patterns because they produce leaves and leaf litter synchronously. The relationships between the leaf or litter traits and the herbivory or decomposition rate were investigated within each of the two types using correlation analyses. The relationship between the herbivory rate and decomposition rate was also evaluated by simple linear regression analyses within each of the two plant types, and the difference in slope between the two types was analyzed using analysis of covariance (ANCOVA).

In all analyses, the variables were $\ln(x + 1)$ -transformed when necessary to meet the assumption of normality. For the herbivory rate, $\ln(1000 \times \text{herbivory rate} + 1)$ was used for transformation because the herbivory rates were very small (Coley 1983).

RESULTS

Leaf and litter traits

Here and throughout, data are presented as mean \pm SD. On average, the total phenolic content per unit area was lower in litter (1.26 ± 1.09 mg/cm²) than in leaves (2.06 ± 1.57 mg/cm²), the condensed tannin content per unit area was lower for litter (0.35 ± 0.27 mg/cm²) than for leaves (0.52 ± 0.56 mg/cm²), and the N content per unit area was lower for litter (0.13 ± 0.05 mg/cm²) than for leaves (0.20 ± 0.07 mg/cm²) (Fig. 1a, c, e). For these compounds, their contents per unit mass showed the same trends: the total phenolic content per unit mass was less for litter ($9.44\% \pm 6.60\%$) than for leaves ($14.4\% \pm 7.29\%$), the condensed tannin content per unit mass was less for litter ($2.74\% \pm 1.74\%$) than for leaves ($3.47\% \pm 2.89\%$), and the N content per unit mass was less for litter ($1.09\% \pm 0.22\%$) than for leaves ($1.66\% \pm 0.37\%$) (Fig. 1b, d, f). On the other hand, the lignin content per unit mass was higher for litter ($18.8\% \pm 4.50\%$) than for leaves ($16.3\% \pm 6.74\%$), although the lignin content per unit area differed little between leaves (2.03 ± 1.08 mg/cm²) and litter (2.37 ± 1.26 mg/cm²) (Fig. 1h, g). Generally, there were strong relationships across the species for these traits for leaves vs. litter (Fig. 1a–h), even though there was substantial scatter for each relationship. In contrast, LMA and toughness differed little between leaves and litter (Fig. 1i, j).

Among the traits, the total phenolic concentration had significant positive correlations with the condensed tannin concentration and LMA and negative correlations with the amount of lignin in the leaves or litter (Appendices C and D). The condensed tannin concentration showed significant negative correlations with the

litter lignin concentration, but the correlation was only marginally significant for leaves. The condensed tannin concentration was also significantly positively correlated with LMA for leaves but not for litter. The lignin concentration was marginally negatively correlated with the N concentration both for leaves and litter. The N concentration had significant negative correlations with LMA both for leaves and litter, and it was also significantly negatively correlated with leaf toughness, but the correlation was only marginally significant for litter. There were significant positive correlations between toughness and LMA for both leaves and litter. The leaf toughness was significantly positively correlated with the ratio of total phenolics and condensed tannins to N, as well as with the C:N ratio. Conversely, litter toughness was significantly positively correlated with the lignin concentration and its ratio to N as well as with the C:N ratio (Appendices C and D). This difference was probably due to the fact that the total phenolic content and condensed tannin content were reduced in litter, whereas most of the lignin remained (Fig. 1a, c, and g). When phylogenetic relatedness was considered, the among-trait relationships for both leaves and litter differed little (Appendices C and D).

Herbivory rate and related leaf traits

The herbivory rate across the species studied ranged from 0.0006% to 0.0676% per day. Only leaf toughness showed a significant negative relationship with herbivory rate across species, as revealed by both correlation (Table 1) and multiple regression analyses. Stepwise multiple regression analyses revealed that leaf toughness explained 22.9% of the interspecific variation in herbivory rate ($R^2 = 0.229$, $P < 0.001$). When phylogenetic relatedness was considered, N concentration, the C:N ratio, and leaf toughness showed significant correlations with herbivory rate (Table 1).

Decomposition rate and related litter traits

The decomposition rates of the species ranged from 0.67 yr^{-1} to 4.85 yr^{-1} , which are values comparable to those in previous studies of tropical rain forests (Santiago 2007). Unlike the herbivory rate, many litter traits were significantly correlated with the interspecific variation in decomposition rate (Table 1). Stepwise multiple regression analysis showed that the best predictor for decomposition rate was a model that included LMA, the lignin to N ratio, and the condensed tannin concentration, and which explained 61.1% of the interspecific variation in decomposition rate; these three traits were negatively related to the decomposition rate for all species ($R^2 = 0.611$, $P < 0.001$). When phylogenetic relatedness was taken into account, the trend for the relationship between each litter trait and the decomposition rate remained unchanged (Table 1).

Herbivory vs. decomposition rates across species

There was no significant relationship between the rates of herbivory and decomposition in the field across

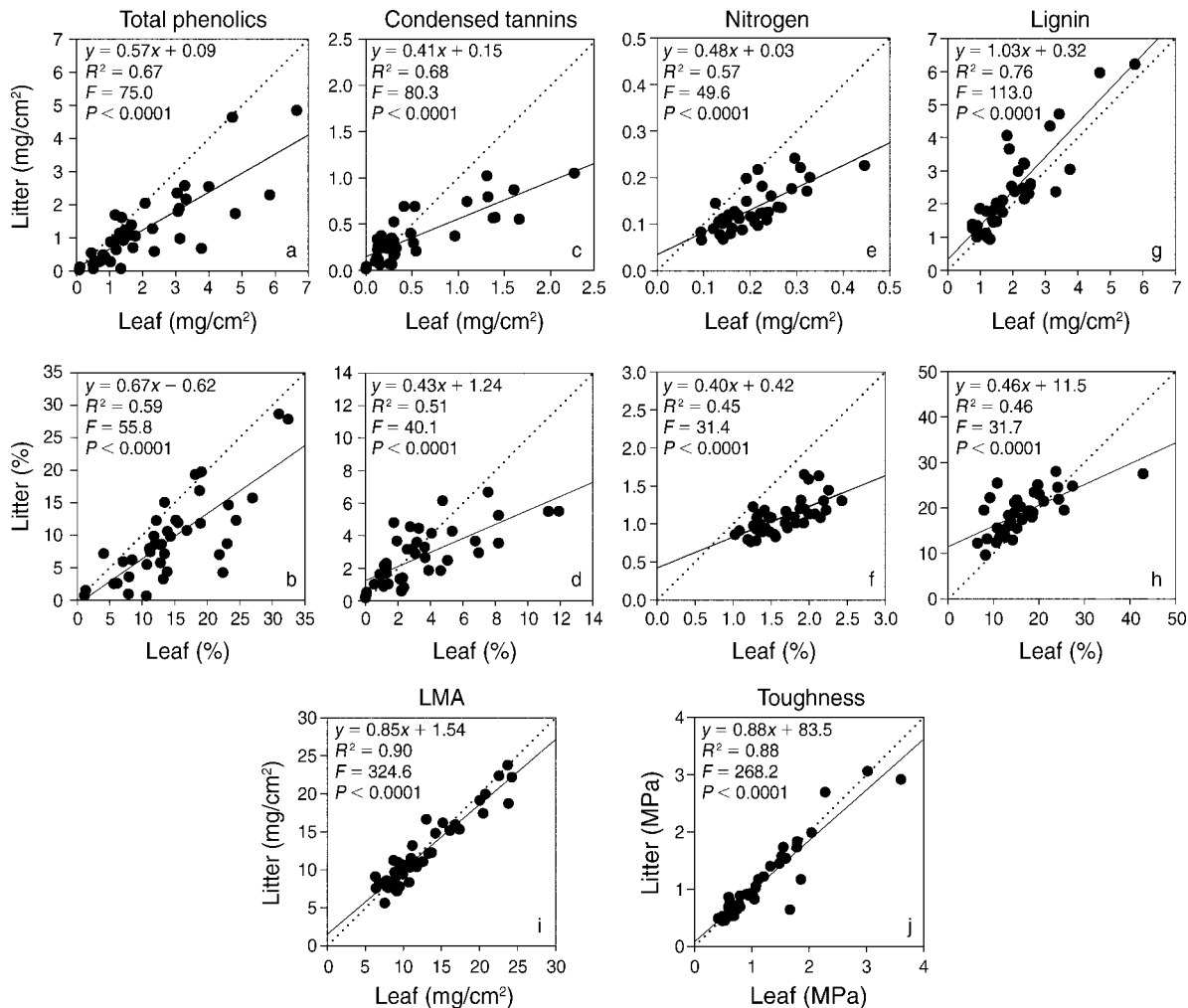


FIG. 1. Relationships between interspecific variation in leaf and litter traits: total phenolic content (a) per unit area and (b) per unit mass (as a percentage of total mass); condensed tannin content (c) per unit area and (d) per unit mass; nitrogen content (e) per unit area and (f) per unit mass; lignin content (g) per unit area and (h) per unit mass; (i) leaf mass per area (LMA); and (j) toughness (originally measured as kilogram-force tested for a leaf sample 3 mm in diameter, converted to SI units of pascals). For each panel, each circle represents a different species. A solid line indicates the regression line for all data. The dotted 1:1 line indicates $y = x$.

TABLE 1. Pearson's correlation coefficients at the species level and phylogenetically independent contrasts (PIC) between leaf traits and the herbivory rate and between litter traits and the decomposition rate.

Variable	Herbivory rate, h ($n = 38$)		Decomposition rate, k ($n = 40$)	
	Species level	PIC	Species level	PIC
Total phenolics	0.013	-0.11	-0.122	-0.01
Condensed tannins	-0.159	-0.10	-0.279†	-0.27†
Lignin	0.103	-0.11	-0.407**	-0.45**
Nitrogen (N)	0.238	0.54***	0.521**	0.55***
Carbon : N	-0.206	-0.54***	-0.473**	-0.57***
Total phenolics : N	-0.082	-0.34	-0.223	-0.16
Condensed tannins : N	-0.217	-0.21	-0.407**	-0.42**
Lignin : N	-0.028	-0.35	-0.552***	-0.57***
LMA	-0.189	-0.25	-0.663***	-0.68***
Toughness	-0.455**	-0.52**	-0.602***	-0.62***

Notes: LMA is leaf mass per area; n is the number of species sampled. Significant correlations are indicated. † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

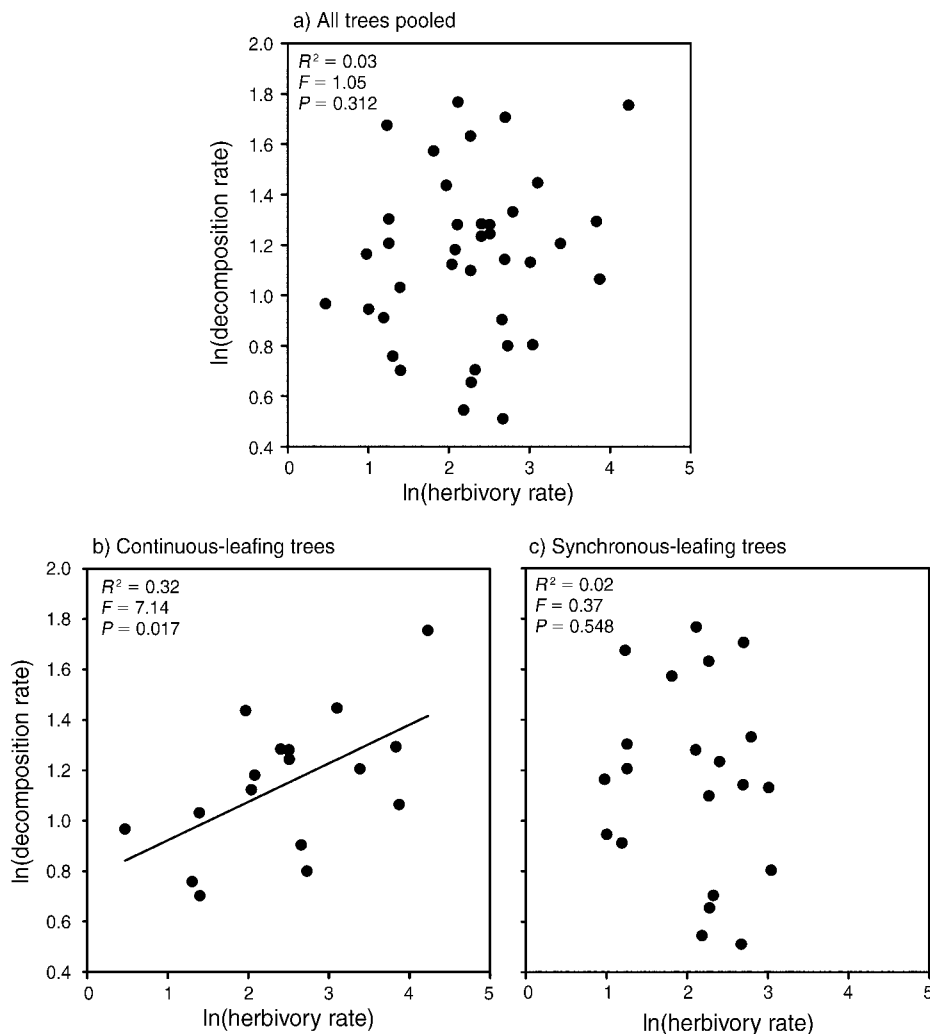


FIG. 2. Relationship between interspecific variation in the herbivory rate investigated for leaves and decomposition rate investigated for litter. Log-transformed herbivory rates were originally measured as percentage of leaves eaten per day; log-transformed decomposition rates were originally measured as yr^{-1} . (a) Relationship for all tree species studied ($y = 0.07x + 1.01$, $n = 38$ species); each circle represents a different species. (b) Relationship for those tree species with a continuous leaf emergence pattern ($y = 0.15x + 0.77$, $n = 17$ species); each circle indicates a species with a relatively small CV (< 0.9). (c) Relationship for those tree species with synchronous leaf emergence patterns ($y = -0.08x + 1.32$, $n = 21$ species); each circle indicates a species with a relatively high CV (≥ 0.9).

species (Fig. 2a). The nature of this relationship remained unchanged when phylogenetic relatedness was considered ($r = 0.12$, $P = 0.479$, $n = 38$ species).

Herbivory vs. decomposition rates within plant types differing in leaf emergence pattern

When the species were segregated according to their leaf emergence pattern, the mean herbivory rate for those with continuous leafing (0.018% per day) was slightly higher than for those with synchronous leafing (0.009% per day), but not significantly so ($P = 0.166$, t test). There was no significant difference in the mean decomposition rate between the two types ($P = 0.910$, t test). No other leaf or litter traits differed significantly between the two types, except for leaf life span, which

was significantly longer in the synchronous-leaving species ($P = 0.02$, t test).

There was a significant positive correlation between the herbivory and decomposition rates for those species with continuous leafing (Fig. 2b). In those species, the herbivory rate was negatively correlated with the foliar condensed tannin to N ratio and leaf toughness, and it was marginally negatively correlated with the foliar condensed tannin concentration (Table 2). The litter decomposition rate was negatively correlated with the condensed tannin concentration and tannin to N ratio in litter, and it was marginally positively correlated with the litter N concentration (Table 2). Thus, herbivory and decomposition were correlated with two of the same traits (Table 2). Conversely, the relationship between the

TABLE 2. Pearson's correlation coefficients between leaf traits and the herbivory rate (h) and between litter traits and the decomposition rate (k) for the continuous- and synchronous-leaving species.

Variable	Continuous-leaving ($n = 17$)		Synchronous-leaving ($n = 21$)	
	h	k	h	k
Total phenolics	-0.020	-0.097	0.028	-0.198
Condensed tannins	-0.480†	-0.536*	0.102	-0.130
Lignin	0.067	0.207	0.103	-0.567**
Nitrogen (N)	0.213	0.465†	0.229	0.648**
Carbon : N	-0.196	-0.222	-0.149	-0.688**
Total phenolics : N	-0.071	-0.177	-0.084	-0.338
Condensed tannins : N	-0.584*	-0.589*	0.058	-0.322
Lignin : N	-0.023	-0.197	-0.003	-0.659**
LMA	-0.353	-0.407	-0.046	-0.783***
Toughness	-0.728**	-0.240	-0.275	-0.744***

Notes: The number of species sampled is given by n . Significant correlations are indicated.

† $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

herbivory and decomposition rates was not significant for those species with synchronous leafing (Fig. 2c). In those species, no traits were significantly correlated with the herbivory rate, whereas, the decomposition rate was negatively correlated with lignin, C to N ratio, lignin to N ratio, LMA, and toughness, and it was positively correlated with the litter N concentration (Table 2). The difference in the regression slopes between the herbivory and decomposition rates for the two types of plants was marginally significant ($P = 0.097$, ANCOVA).

DISCUSSION

Our data indicate no strong association between the herbivory and decomposition rates across tree species in a tropical rain forest, which is opposite to what was expected based on previous laboratory and field studies in nontropical systems (Grime et al. 1996, Cornelissen et al. 1999, 2004, Wardle et al. 2002), even though we found large interspecific variation in both rates (Fig. 3). This is because the leaf and litter traits related to herbivory and decomposition in the field were inconsistent (Table 1). Correcting for the phylogenetic relatedness among the species did not influence the association between the rates of herbivory and decomposition. Phylogenetic relatedness may affect the relationships between leaf traits and herbivory rate, but not those between litter traits and decomposition rate. In contrast, when the relationships within plant types differing in their leaf emergence patterns were considered, we found a significant positive relationship between herbivory and decomposition for those species with continuous leafing.

Leaf and litter quality

Contents of total phenolics and condensed tannins were lower for litter than for leaves, probably due to degradation or leaching (Gallet and Lebreton 1995, Kraus et al. 2003). Foliar N content also decreases during senescence because of resorption (Aerts 1996). The lignin concentration was higher for litter than for leaves, probably because the lignin itself remained largely unchanged while the other chemicals decreased. There was substantial scatter in the interspecific

relationships between leaves and litter for these chemicals, probably because of the differences in N resorption ability or the manner of degradation or leaching due to the structure of phenolic compounds among species. However, these chemicals were generally correlated between leaf and litter across species. The leaf traits such as LMA and toughness differed little when leaves turn to litter across species. Thus, the interspecific variation in leaf quality is tightly correlated with that in litter quality.

Herbivory

The herbivory rates estimated in this study were lower than those estimated by Coley (1983), who found rates of 0.24% per day for mature leaves of pioneer species and 0.04% per day for mature leaves of persistent species in a tropical rain forest on Barro Colorado Island, Panama. This may be because Coley's study was conducted on saplings in the understory, where herbivory damage is generally higher (Coley and Barone 1996). However, the leaf trait relating to herbivory was

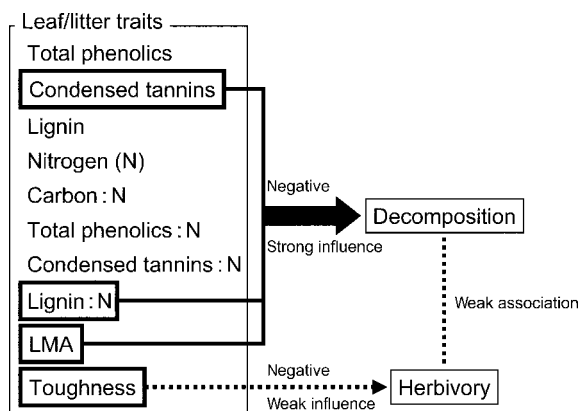


FIG. 3. Relationships between herbivory and decomposition rates across tree species and leaf and litter traits related to these rates in a Malaysian tropical rain forest. Solid, wide arrows indicate a strong influence, dashed arrows indicate a weak influence, and dashed lines indicate a weak association.

consistent; Coley (1983) also found that for saplings of 46 Neotropical tree species, the herbivory rate on mature leaves was negatively correlated with leaf toughness, but not with total phenolics, condensed tannins, or lignin. Phenolic compounds are thought to be a general defense, and many studies have demonstrated their negative effects on herbivores (e.g., Bryant et al. 1987, Wainhouse et al. 1990, Shimada and Saitoh 2003). However, Ayres et al. (1997) suggested that the extensive structural variation of condensed tannins causes them to differ markedly in their antiherbivore activity, and the same tannins can have different effects on different herbivores, presumably because of interactions between tannin structure and gut physiology. For this reason, phenolic compounds may not be a general defense and cannot explain the interspecific variation in herbivory rate, especially for highly diverse herbivore communities in which there is a high proportion of specialist herbivores.

Leaf toughness seems to be a most effective defense across species (Table 1; see also Coley 1983), but it explains only about 23% of the interspecific variation in herbivory rate explored by multiple regression analysis in this study. This is probably due to the fact that herbivory across species under natural conditions involves several factors, including specialized plant–herbivore interactions and differences in plant accessibility to herbivores. The phylogenetic analyses in this study showed that the N concentration and C:N ratio had positive and negative significant correlations with the herbivory rate, respectively, whereas these relationships disappeared when all species were considered as statistically independent data points. This suggests that the C:N ratio in leaves is related to herbivory within closely related trees and that the nature of these relationships depends on the taxon considered, implying that plant–herbivore interactions are taxon specific (Novotny et al. 2002, Lewinsohn et al. 2005). Moreover, leaf toughness is a compound trait influenced by a leaf's chemical and physical properties, and here, it was positively correlated with the ratios of C, total phenolics, and condensed tannins to N and LMA. Hence, plants may have an effective defensive strategy against herbivores based on a number of classes of secondary metabolites or a combination of physical, chemical, and developmental defenses (Kursar and Coley 2003). Interestingly, lignin was not correlated with leaf toughness, even though fiber content in leaves is thought to be related to leaf toughness and defensive effects against some insects (Wainhouse et al. 1990, Choong et al. 1992). Lignin may play a defensive role against pathogens rather than herbivores (Loehle 1988).

There remains a possibility that other leaf traits not measured in this study, such as the concentrations of alkaloids or other chemicals, could be responsible for the interspecific variation in herbivory rate. However, it is more plausible that the range of defensive strategies in this forest is highly diverse due to the high level of tree

diversity. Therefore, the herbivory rate across species may not be strongly related to single leaf traits in this ecosystem.

Decomposition

In contrast to the herbivory rate, the litter decomposition rate across species was easily explained by many single litter traits, including the lignin and N concentrations, leaf toughness, LMA, and the ratios of C, condensed tannins, and lignin to N. These data are consistent with those from several earlier studies (Melillo et al. 1982, Horner et al. 1988, Gallardo and Merino 1993, Cornelissen 1996). In particular, the lignin to N ratio, LMA, and condensed tannin concentration collectively regulated the decomposition rate across species. The difference in the relationships between herbivory and decomposition with plant traits may reflect differences in the nature of the interactions between plants and herbivores, and between plants and decomposers. During decomposition, organic chemical and nutrient dynamics change in the litter, and decomposers selectively consume different organic chemicals (Berg and McClaugherty 2003) until the plant litter disappears. Compared to plant–herbivore interactions, plant–decomposer interactions are less specific and can be governed by litter chemicals. This may be because plant–decomposer interactions have relatively little effect on plant fitness in comparison to plant–herbivore interactions.

There was a slight mismatch between the measurements for herbivory and decomposition in the field. The herbivory rates were measured under more natural conditions; however, the decomposition rates were still measured under standardized conditions in the field. We expected that the results would not differ greatly if the litter were decomposed in more natural conditions (e.g., below the tree of origin), because a recent meta-analysis suggested that decomposition is dominantly driven by species litter quality within biomes worldwide (Cornwell et al., *unpublished manuscript*). Therefore, the different drivers of herbivory and decomposition in the field are likely to originate from inherent differences in the processes of herbivory and decomposition in this ecosystem.

Factors affecting the association between herbivory and decomposition

In contrast to phylogenetic relatedness, leaf emergence patterns appear to affect the association between herbivory and decomposition. We found a significant positive relationship between herbivory and decomposition rates for the continuous-leaving species, but not for the synchronous-leaving species. Previous studies have suggested that leaf emergence patterns are related to plant defensive strategies (Coley and Barone 1996, Kursar and Coley 2003). Based on a survey of defensive traits in young leaves from several unrelated species in the understory of a tropical forest, Kursar and Coley

(2003) suggested that, although species fall along a continuum, two types of defensive strategies (escape and defense) occur, each with a different set of defensive traits. Escape species expand their leaves rapidly to minimize the period during which they are vulnerable to herbivores, delay chloroplast development until the leaf is full size, and produce leaves synchronously to satiate specialist herbivores. In contrast, defense species rely on a number of effective chemical defenses, expand their leaves slowly with normal chloroplast development, and produce leaves continuously rather than synchronously. In our study, we did not measure the traits of young leaves, and no leaf trait differed between the two types identified according to leaf emergence pattern except for leaf life span. However, immobile defensive traits (Coley et al. 1985) such as phenolics in mature leaves could be holdovers from defensive traits in young leaves. Thus, the interspecific variation derived from the leaf emergence patterns in the defensive traits of young leaves may affect the interspecific variation in mature leaves, and even that in litter.

Similarly, Chapman et al. (2006) suggested that the different functional types of trees (e.g., evergreen vs. deciduous) often respond differentially to herbivores and could cause different changes in litter quality. Evergreen trees often have a high baseline concentration of constitutive phenolic compounds (vs. investment in growth) usually stored in structural tissues, which renders it less mobile. In contrast, deciduous trees adopt induced defenses, such as condensed tannins, in response to herbivores, because they usually invest more in growth. These species store carbon in their roots and perennial tissues, thus allowing them flexibility in allocation to defensive phenolics. Although all of our study trees were evergreens, we found that the herbivory rate in the continuous-leafing species was negatively correlated with both the condensed tannin to N ratio and leaf toughness. Thus, in light of these hypotheses (Kursar and Coley 2003, Chapman et al. 2006), the continuous-leafing species may be more likely to have some condensed tannins that are effective in deterring herbivores, particularly generalists, because the plants do not escape temporally. Furthermore, the negative relationship between the foliar condensed tannins and herbivory implies that there might be a growth–defense trade-off in the context of the allocation to defensive phenolics for those species (Coley et al. 1985). Moreover, a high condensed tannin concentration and its ratio to N in litter reduced the decomposition rate, accounting for the positive relationship between herbivory and decomposition in those species.

We found no such trend for the synchronous-leafing species. Synchronous-leafing species may be more likely to have induced defenses. Therefore, these chemical (e.g., condensed tannins) concentrations in intact leaves may not have strong relationships with herbivory or decomposition rates in those species. Such differences in continuous and synchronous leafing may drive the

difference in the relationship between herbivory and decomposition based on leaf emergence patterns. That is, the leaf emergence patterns may affect not only the relationship between leaf traits and the rate of herbivory, but also that between litter traits and the rate of decomposition. Wardle et al. (1998, 2002) indicated that the relationship between palatability or the vegetation response to herbivores and decomposition within a plant group (e.g., herbs and trees) is not particularly strong. Our data also showed no significant relationship between herbivory and decomposition across tree species. However, our results for the two leaf emergence types suggest that a plant functional type (leaf emergence pattern) within a plant group (in this case, trees) may influence the association between herbivory and decomposition, although additional studies are necessary.

Conclusion

Previous studies have shown that leaf palatability to herbivores may be related to litter decomposability, and that herbivores can significantly influence aboveground and belowground feedback in such ecosystems as semiarid woodlands and boreal and temperate forests (Pastor and Naiman 1992, Wardle et al. 2002, Chapman et al. 2003). However, in tropical rain forests, decomposition rate across species is not easily predicted by herbivory rate, even though the rate is determined by a set of traits related to aboveground interactions (e.g., photosynthetic rate; Santiago 2007). This is probably because plant diversity results in diverse plant–herbivore interactions, suggesting that well-defended leaves are not necessarily decomposed slowly when they turn to litter. Furthermore, the relationship between herbivory and decomposition may be more influenced by functional types (e.g., leaf emergence pattern) than by phylogenetic relatedness. The implication of these results is that the effects of herbivory on carbon and nutrient cycling are likely to depend on plant species that mediate interactions between herbivores and decomposers in species-rich tropical rain forests. As such, and as opposed to other ecosystems, herbivores may not necessarily generate positive feedback for carbon and nutrient cycling in these diverse forests.

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APPENDIX A

Summary of the composite phylogenetic tree assembled for all tree taxa in a previous study looking at the relationship among various types of leaf traits in tropical rain forests in Borneo, Malaysia (*Ecological Archives* E089-149-A1).

APPENDIX B

Selected species, their leaf life span, and CV of the ratio of number of new leaves to number of total leaves marked previously per unit time per species (*Ecological Archives* E089-149-A2).

APPENDIX C

Pearson's correlation matrix of leaf traits at species level and at phylogenetically independent contrasts (*Ecological Archives* E089-149-A3).

APPENDIX D

Pearson's correlation matrix of litter traits at species level and at phylogenetically independent contrasts (*Ecological Archives* E089-149-A4).