

Explaining Leaf Herbivory Rates on Tree Seedlings in a Malaysian Rain Forest

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ABSTRACT

Seedlings of five species of dipterocarp trees were planted in experimental plots in rain forest gaps in Sabah, Malaysia, and the rates of herbivory on their mature leaves recorded over 6 mo. A novel method was used to estimate the feeding pressure exerted by the local insect herbivore community, derived from the relative abundances of the dominant generalist herbivores and their feeding preferences. Characteristics of the leaves related to their defense and nutritional value were measured—phenolic content, laminar fracture toughness, laminar thickness, and nitrogen content. Three main groups of herbivorous insects were present—coleopteran and lepidopteran herbivores, which were sampled by hand from the seedlings, and orthopteran herbivores, which were sampled by sweep netting. The feeding preferences of the main coleopteran and orthopteran herbivores were determined using laboratory feeding trials. Combining variables in a Principal Components Analysis, a clear separation was found between the five seedling species along the first extracted component. This correlated closely with herbivory rates between species. The first extracted component comprised a negative influence of phenolic content and positive effects of nitrogen content, laminar fracture toughness, abundances of coleopteran and lepidopteran herbivores, and estimated feeding pressure of the coleopteran community. Further studies are required to determine the potential applications of the latter measure of estimated herbivore community impact.

Key words: community feeding pressure; dipterocarp; feeding preference; leaf fracture toughness; nitrogen; phenolics; Sepilok, Sabah.

INSECTS ARE THOUGHT TO BE RESPONSIBLE FOR AROUND 70 PERCENT OF ALL HERBIVORE DAMAGE IN THE TROPICS (Coley & Barone 1996), but relating rates of herbivory to the insect communities present is often problematic due to the large number of herbivorous insects in the tropics and the difficulties of capturing and identifying them. In addition, there are numerous features of plant species that influence their rates of herbivory, both in terms of their defenses and nutritional value. Few studies have combined these measures in order to determine the principle characteristics of rain forest trees that determine the rates of herbivory that they receive.

Emerging evidence suggests that generalists form a large proportion of rain forest insect herbivore communities, especially among folivores, and that relatively few species dominate communities (Novotny & Basset 2005). If generalized feeding is common, herbivore preferences will play a crucial role in determining the amount of damage received by a given plant species. Moreover, nonspecific leaf defenses that deter generalist feeders would be favored rather than those targeted against specialist herbivores. Feeding preferences are likely to be determined by a combination of responses to primary nutrients and secondary compounds (Bernays & Chapman 1994).

Plants employ both chemical and physical defenses against herbivores. Phenolic compounds are known to be effective herbivore deterrents (Bernays 1991; Bernays & Chapman 1994). In general,

they are thought to act as digestibility reducers rather than through direct toxicity. The compounds making up the total phenolic content of plant tissues and their relative concentrations vary between species. The deterrent effect of phenolics represents the combined and potentially synergistic action of a suite of related chemicals, which may have variable influences on insect feeding (Appel 1993).

In terms of physical defense, the property of a leaf that best describes its ability to resist the action of insect feeding is fracture toughness, which measures the force required to create a running fracture in a material (Sanson *et al.* 2001). Thick leaves may pose an obstacle to insects with smaller mandibles or musculature (Bernays 1991).

Nutrient content of leaves can also influence insect feeding. Since defenses pose constraints on the digestion and processing of leaf material, nutrients may compensate for this and alter the relative preferences of generalist feeders. Nitrogen is a limiting resource for herbivores and numerous studies have demonstrated its influence upon the feeding preferences and performances of herbivores (*e.g.*, McNeill & Southwood 1978, Athey & Connor 1989), although its importance in determining rates of herbivory is less definitive. As plants balance investment in growth and defense, high nitrogen content is typically associated with fast growing but poorly defended tissues (Herms & Mattson 1992).

This study examines whether the variability in herbivory rates observed on seedlings in a tropical rain forest can be accounted for by aspects of their defensive and nutritional characteristics, and how this is related to the insect herbivore communities found on and around them. We aimed to test the following predictions: (1) that

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the rates of herbivory suffered by seedlings would be positively correlated with nitrogen content and negatively with levels of chemical and physical defense; and (2) that the feeding preferences of the main generalist herbivores would be correlated with the rates of damage observed in the field.

METHODS

STUDY SITE.—The Kabili-Sepilok Forest Reserve (5°10' N, 117°56' E), Sabah, Malaysia, is a largely intact 4294 ha fragment of coastal rain forest set amongst a matrix of cultivated land and secondary forest. The majority of the reserve is comprised of alluvial soils 15–30 m asl, with forests dominated by canopy trees of *Parashorea tomentella* (Sym.) Meijer, *Shorea johorensis* Foxw. (Dipterocarpaceae), and *Eusideroxylon zwageri* Teijsm. & Binn. (Lauraceae).

STUDY SPECIES.—Five species of dipterocarp were chosen to test the effect of habitat specialization on their responses to different environmental conditions as part of a larger experiment (see Eichhorn *et al.* 2006 for further details). Three species are naturally restricted to alluvial soils: *Hopea nervosa* King. (local name: selangan jangkang), *P. tomentella* (Sym.) Meijer (urat mata beludu) and *Shorea fallax* Meijer (seraya daun kasar); two further species are sandstone specialists: *S. multiflora* (Burck) Sym. (banjutan) and *H. beccariana* Burck (selangan penak). Seedlings of alluvial species were collected from Danum Valley during mast fruitings in various years, potted in 2 × 8" bags, and stored under 30 percent shade-cloth in the FACE (Forests Absorbing Carbon Emissions) project nursery until January 2000. They were transferred to the Forest Research Centre nursery, Sepilok, and stored beneath two layers of 80 percent shade-cloth from January to March 2000. Seedlings of sandstone species were collected as wildlings from the understory in Sepilok from March to May 2000.

EXPERIMENTAL DESIGN.—Four plots were established in natural treefall gaps from 400 to 600 m² in alluvial lowland forest between March and June 2000. The remains of trunks and branches and all plants above 50 cm in height were removed. In one plot, overhanging branches were removed from neighboring trees. Thirty seedlings of each of the five species were planted in a randomized block design in each plot, half of which were fertilized biannually with 12 g of Agroblen (SCOTTS) slow-release complete fertilizer (16N : 8P : 9K : 3Mg + trace elements).

LEAF CHEMISTRY.—Leaves were collected in April 2002. Three seedlings of each species and fertilizer treatment were randomly selected within each plot. Several undamaged mature leaves of varying age were sampled haphazardly from each plant, dependent upon leaf size (two large leaves for *P. tomentella*, three for *H. nervosa* and *S. fallax* and up to five smaller leaves from *S. multiflora* and *H. beccariana*).

Leaves were dried for 48 h at 60°C and then transported to the UK in sealed plastic bags. Prior to processing, they were dried

for a further 48 h at 60°C. Leaves from individual plants were bulked for processing. They were ground entire in a fine particulate mill and stored in airtight glass vials. Phenolics were assayed using the Folin-Ciocalteu method (Waterman & Mole 1994), which gives the percentage of leaf dry weight made up of tannic acid equivalents. To assess nitrogen content, leaf material was digested using the sulphuric acid–hydrogen peroxide procedure and assayed using the Kjeldahl method (Allen 1989).

MECHANICAL PROPERTIES OF SEEDLINGS.—Measurements took place in June–July 2002. Three unfertilized seedlings per species were randomly selected within each plot, and three undamaged mature leaves selected haphazardly from the top, middle, and bottom of each. Leaves were collected in the early morning, placed in damp airtight plastic bags and stored at 4°C for 2 h; measurements were taken within 12 h. Each leaf was initially cut longitudinally along one side of the midrib. A screw-gauge micrometer was used to record the thickness of the discarded portion of lamina, avoiding prominent veins.

Measurement of fracture toughness used the equipment described by Darvell *et al.* (1996) and the method of Lucas and Pereira (1990). Three cuts were made around the midpoint of each leaf, at 90° to the midrib, including both the midrib and a secondary vein. In most cases, the toughness of the section of lamina between the secondary vein and the midrib was used to determine laminar fracture toughness (LFT). A force-displacement plot was used to distinguish the secondary vein and midrib from the lamina; all veins were assumed to be circular. A correction was made for blade friction. Blades were cleaned with isopropanol between leaves, although some required more frequent cleaning. Data collected over 2 mo suggested no decrease in scissor sharpness occurred.

INSECT COMMUNITY VARIABLES.—Collections took place in both dry (May–Jul 2001) and wet seasons (Jan–Mar 2002). Records were combined as this increased the total sample size and allowed an estimation of community structure over a longer time period. Plots were surveyed between 0630 h and 1300 h. Orthopterans were collected by sweep netting within 1.5 m of the plot edges to prevent damage to the experimental seedlings. Three seedlings of each species and fertilizer treatment were randomly selected and all plant parts were visually searched. Coleopteran and lepidopteran larval abundance were calculated as the number of individuals per 1000 leaves; leaf counts were conducted by R. Nilus (pers. comm.). Confirmation of feeding on the source species was obtained for all individuals in the laboratory. Insect species that failed to feed on leaves of the source plant were removed from the analysis.

All coleopterans and orthopterans were placed into feeding trials within 12 h of capture. Seven species of dipterocarp were used—the five species above, plus two locally abundant species, *Dryobalanops lanceolata* Burck. (kapur paji) and *Shorea leprosula* Miq. (seraya tembaga). Plant material was collected from nursery seedlings grown in their native soil type. The midrib and edges of leaves were removed and equal size segments of each species placed in Petri dishes with a single insect. Trials were terminated after 4 d. Ability to feed on a particular species was recorded only if

a sustained feeding bout occurred, and although it was common for leaf segments to be sampled around the edges, this was not recorded as feeding. The percentage of sustained feeding bouts on a given dipterocarp species over all trials of an insect species was used to estimate its feeding preferences. Data on area removed did not produce qualitatively different results.

A small number of species dominated the coleopteran and orthopteran communities and were therefore used to estimate community feeding pressure. The aim was to produce a simple composite variable describing the effects of a number of insect herbivore species within a local community. Seven orthopteran species comprised 89 percent of individuals confirmed as potential herbivores and four species of weevil accounted for 87 percent of coleopterans. All 11 species were generalists capable of feeding on leaves of all species tested. There were no apparent differences in feeding preferences between orthopteran adults and nymphs. To estimate community feeding pressure on a seedling species in a given plot, the estimated feeding preference of an insect herbivore for that species was weighted by its relative abundance within the plot and these values were summed across herbivore species. This was scaled from 0 to 100, representing a percentage risk of herbivory.

HERBIVORY.—Five unfertilized seedlings of each species per plot were randomly selected from those that had not been used in the insect collections. Up to 30 leaves were surveyed per seedling, sampled at regular points throughout the canopy. Leaves were numbered using an indelible marker pen, close to the midrib and *ca* 1 cm from the petiole. Senescent or heavily damaged leaves (mechanical or fungal) were excluded. Two surveys were conducted (Sep–Oct 2001 and Apr–May 2002). Herbivory was scored using a practiced estimate of lamina damage based on percentage classes (0%, < 2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–100%). Damage was defined as removal of potential photosynthetic tissue, including leaves rolled or sewn together, even if not entirely eaten. Where damage during development had disfigured a leaf, its potential leaf area was considered to be the same as its closest neighboring entire leaves and the total damage to be the difference between its potential and actual leaf area. Absent leaves were discounted, unless the petiole was still attached, since it was seldom possible to attribute abscission to the action of herbivores. Analysis of a subset of data for each species suggested no association between the amount of damage on a leaf and the likelihood that it would be present in the following survey. Accuracy of estimates was confirmed on a subsample of leaves from each species using a grid scale and by intermittent repeatability checks. Rates of herbivory per month were calculated from the difference in damage levels on individual leaves between surveys using the midpoints of the percentage damage classes, divided by the number of months between surveys.

STATISTICAL ANALYSIS.—Mean values for all variables were calculated per plot. Phenolic content, nitrogen content, and herbivory rate were arcsine-transformed prior to analysis; an increment (0.015) was added to the herbivory rates to permit transformation. Species comparisons were made using ANOVA, or Kruskal–Wallis if non-normal. A Principal Components Analysis (PCA) was used

to identify relationships between variables. An initial correlation matrix was examined; coefficients greater than 0.8 imply singularity, *i.e.*, a single variable has an overriding effect. Correlations were calculated using Pearson's coefficient, which assumes a linear relationship; this was confirmed by graphical examination. Variables that correlated with no others were removed and the analysis was repeated. Derived variables were extracted if they had eigenvalues greater than one and the scree plot of eigenvalues indicated that they were reliably distinct from the remaining variance (Cattell 1966). With small sample sizes, four or more loadings greater than 0.6 are required for an extracted component to be reliable (Guadagnoli & Velicer 1988). Linear regression was used to correlate components with herbivory rates.

RESULTS

There were no significant effects of fertilization on any variable in this study (ANOVA or Kruskal–Wallis, $P > 0.05$ for all tests). This study formed part of a larger experiment in which no effects of fertilizer addition were found on growth of seedlings (R. Nilus, pers. comm.), leaf nutrients (D.H. Dent, unpublished data), or herbivory rates (Eichhorn *et al.* 2006). Data from fertilized and unfertilized seedlings were therefore combined.

The variables recorded from the seedlings are summarized in Table 1. There were significant differences between species in phenolic content ($F_{4,15} = 52.6$, $P < 0.001$), LFT ($F_{4,15} = 6.80$, $P = 0.002$), and laminar thickness ($\chi^2 = 9.78$, $df = 4$, $P = 0.044$), but not in nitrogen content ($F_{4,15} = 2.72$, $P = 0.069$). Among the insect community variables, species varied in abundance of coleopterans ($\chi^2 = 14.5$, $df = 4$, $P = 0.006$), abundance of lepidopterans ($\chi^2 = 13.4$, $df = 4$, $P = 0.010$), estimated feeding pressure of coleopterans ($\chi^2 = 17.6$, $df = 4$, $P = 0.001$), and estimated feeding pressure of orthopterans ($F_{4,15} = 128$, $P < 0.001$). The rates of herbivory also varied among species ($F_{4,15} = 10.3$, $P < 0.001$).

When entered into a PCA, all variables correlated significantly with at least one other, but the greatest correlation coefficient was 0.659, indicating singularity was not a problem within this data set. Two principal components had eigenvalues greater than one and were extracted in full. Inspection of the scree plot of components confirmed that these were reliably distinct from the remainder of the variance. The contribution of each variable to the extracted components is summarized in Table 2. Nitrogen had the weakest contribution, with only 42.7 percent of variance accounted for.

The first extracted component (PC1) was determined largely by phenolic content, which was negatively related to both LFT and nitrogen content. In addition, the abundance of coleopteran and lepidopteran herbivores and the estimated feeding impact of coleopterans were strongly negatively related to the phenolic content of the leaves. The second component (PC2) contained only three factor loadings greater than 0.6 and was therefore potentially unreliable. Nevertheless, LFT and laminar thickness were negatively correlated, and the estimated feeding pressure of orthopterans was negatively correlated with LFT. The five dipterocarp species were

TABLE 1. Variables recorded from seedlings; mean \pm SE, $N = 4$ for all values. Species: Hn = *Hopea nervosa*; Pt = *Parashorea tomentella*; Sf = *Shorea fallax*; Sm = *S. multiflora*; Hb = *H. beccariana*. Significance levels determined using (i) ANOVA (ii) Kruskal–Wallis; ns = $P > 0.05$ (not significant), * = $P < 0.05$ (significant), ** = $P < 0.001$ (highly significant), *** = $P < 0.001$ (very highly significant).

Variable	Units	Species					Significance
		Hn	Pt	Sf	Sm	Hb	
Phenolics	% DW	16.3 \pm 0.3	8.8 \pm 1.0	8.1 \pm 0.4	21.1 \pm 1.0	17.5 \pm 0.9	***(i)
Laminar fracture toughness	J/m ²	611.3 \pm 49.2	643.4 \pm 32.3	467.7 \pm 41.8	413.3 \pm 32.7	551.0 \pm 23.3	***(i)
Laminar thickness	mm	0.17 \pm 0.01	0.19 \pm 0.02	0.20 \pm 0.03	0.23 \pm 0.01	0.16 \pm 0.01	*(ii)
Nitrogen content	mg N/g DW	7.3 \pm 0.1	7.5 \pm 0.3	7.1 \pm 0.2	6.8 \pm 0.1	6.9 \pm 0.1	ns (i)
Coleopteran abundance	n/1000 leaves	10.6 \pm 3.5	12.4 \pm 1.9	8.1 \pm 3.8	0.7 \pm 0.5	0.6 \pm 0.2	** (ii)
Lepidopteran abundance	n/1000 leaves	10.0 \pm 2.8	36.4 \pm 9.2	9.0 \pm 1.4	3.9 \pm 2.1	2.2 \pm 0.5	*(ii)
Coleopteran feeding pressure	% risk	27.9 \pm 0.3	23.9 \pm 0.2	29.1 \pm 0.2	8.7 \pm 3.3	15.2 \pm 1.6	** (ii)
Orthopteran feeding pressure	% risk	22.6 \pm 1.7	47.9 \pm 1.3	59.2 \pm 0.5	44.6 \pm 1.3	34.6 \pm 1.0	***(i)
Herbivory rate	%/mo	0.19 \pm 0.07	0.56 \pm 0.07	0.25 \pm 0.07	0.01 \pm 0.00	0.16 \pm 0.04	***(i)

clearly separated by both PC1 ($F_{4,15} = 30.4$, $P < 0.001$) and PC2 ($F_{4,15} = 13.2$, $P < 0.001$). Rate of herbivory on the five species was significantly correlated with PC1 ($R^2 = 0.860$, $N = 5$, $P = 0.023$; Fig. 1), but not with PC2 ($R^2 = 0.321$, $N = 5$, $P = 0.319$).

DISCUSSION

The clear separation between seedling species within the analysis, and the correlation of herbivory rates with PC1, indicates that the variables studied can explain a significant proportion of the variation in documented rates of herbivory. It has already been demonstrated

that species identity is the principal determinant of herbivory rates in this system, regardless of environmental conditions (Eichhorn *et al.* 2006), a finding that has been documented elsewhere (*e.g.*, Howlett & Davidson 2001). The analysis presented here provides a basis for understanding of this separation between the species in the context of both their characteristics and the insect herbivore communities upon them.

Phenolic defense would appear to be the underlying factor determining both the abundance and estimated feeding pressure of the dominant insect herbivores, and thereby the rates of herbivory they cause. A negative association was found between foliar nitrogen and phenolic content. This seems to be a common pattern within communities of tropical trees (Turner 2001). High nitrogen content is associated with fast growth, while high levels of chemical defenses are characteristic of slower-growing plants (Herms & Mattson 1992). Furthermore, it has been demonstrated that high

TABLE 2. Eigenvalues, percentage of total variance explained and factor loadings for the first two principal components extracted from the listed variables. Factor loadings greater than 0.6 marked in bold.

Principal components	1	2
Eigenvalue	3.44	1.97
% variance	42.95	24.61
Variable	Factor loading	
Defence		
Phenolic content	-0.75	-0.54
Laminar fracture toughness	0.71	-0.60
Laminar thickness	-0.34	0.76
Nutritional value		
Nitrogen content	0.63	0.17
Insect community		
Coleopteran abundance	0.86	-0.09
Lepidopteran abundance	0.75	0.04
Coleopteran feeding pressure	0.73	0.12
Orthopteran feeding pressure	0.16	0.83

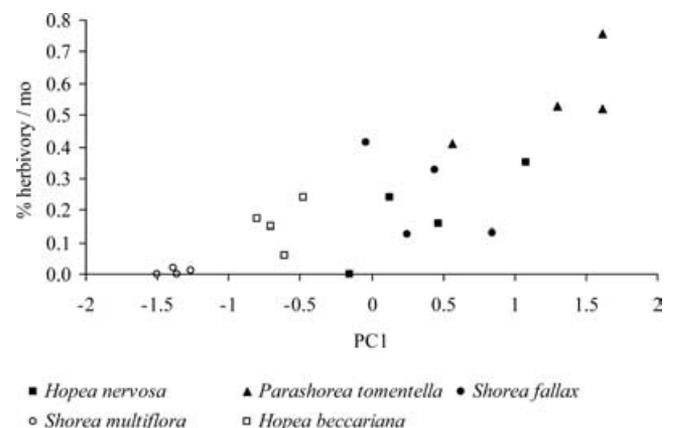


FIGURE 1. Rates of herbivory on mature leaves of five species of dipterocarp in four gaps against the first extracted component from Principal Component Analysis of potential explanatory variables.

levels of nutrient supply reduce the ability of tropical tree seedlings to induce increases in phenolic content following herbivory (Massey *et al.* 2005). Tropical trees employ an array of chemical defenses against herbivores (Coley & Barone 1996, Turner 2001), to which our estimation of gross phenolic content is only an approximation. Nevertheless, in comparisons of multiple leaf traits across a range of plant species, the majority of tropical studies have identified phenolics (as measured by the Folin assay) to be the key determinant of herbivory (*e.g.*, Newbery & de Foresta 1985, Feller 1995, Marquis *et al.* 2001). Exceptionally, Coley (1983) found no relationship with foliar phenolics, but rather one with leaf 'toughness.'

It is impossible to draw conclusions about the influence of nitrogen on the insect community, as it explained little of the variation in the PCA analysis and there was no evidence of variation between species. Nitrogen content can also vary with leaf age (Massey *et al.* 2005) and light levels (Traw & Ackerly 1995) and since these were not controlled for in sampling, this may have confounded our results. In a PCA of leaf traits comparable with the present study, Marquis (2001) nonetheless found the effect of nitrogen on herbivory rates of mature leaves to be minor compared to that of phenolics. Filip *et al.* (1995) related mature leaf herbivory rates to nitrogen content for all but one species in their study. In contrast, others have found no relationship between foliar nitrogen content and herbivore damage (Newbery & de Foresta 1985, Feller 1995), although these studies compared standing levels of damage rather than rates. Leaf water content may be a related factor as it has implications for nitrogen assimilation and accumulation rates (Scriber 1977).

The positive relationship between LFT, herbivory, and the insect community variables contradicts our expectation that it would act as a defense against herbivores. Although it has been said that toughness is a more effective defense than chemical toxins in deterring herbivory (Coley & Barone 1996), in studies using a penetrometer, few have found a significant correlation with herbivory (Coley 1983, Lowman & Box 1983), while the majority found none (Ernest 1989, Feller 1995, Filip *et al.* 1995, Blundell & Peart 1998, Howlett & Davidson 2001, Marquis *et al.* 2001, Spiller & Agrawal 2003).

Abundances of coleopteran and lepidopteran herbivores were both linked with observed rates of damage. Although we would intuitively expect this to be the case, it has seldom been demonstrated. No correlations between insect herbivore abundances and herbivory were found in a range of tropical forests from lowland (Marquis 1991) to mid-montane (Basset & Hoft 1994) and for all but one species in a montane cloud forest (Williams-Linera & Herrera 2003). Increased litter cover around seedlings increased their levels of herbivory (Benitez-Malvido & Kossmann-Ferraz 1999, Garcia-Guzman & Benitez-Malvido 2003), which was postulated to be due to an increased abundance of insects sheltering in the litter. In all these studies, standing damage was recorded rather than rates of herbivory, which may confound results as low herbivore abundance can still generate large amounts of damage on long-lived leaves over time.

Relatively few studies have directly recorded the foliar abundances of herbivores. Chung *et al.* (2002) found a correlation

between standing levels of herbivory and foliar coleopteran abundance among four forest types in Sabah, Malaysia. Their measures of herbivory were, however, made on only 10 leaves for each insect community sample, collected by fogging. Basset (1991) found that standing levels of herbivory in the canopy of an Australian rain forest tree were correlated with the abundance and biomass of lepidopteran larvae, but not with any other major group of herbivores. Again, restricted canopy fogging was used, which did not permit confirmation of folivory. An association for lepidopteran larvae is easier to find than with more actively mobile herbivores as they can usually be assumed to be feeding. More studies are essential to interpret the dynamics of tropical insect herbivore communities and their impact on plants (Burslem *et al.* 2005).

Evidence is mounting that a small number of generalized herbivore species may have a substantial impact upon plants in any given rain forest (Novotny & Basset 2005). The estimated feeding pressure of coleopterans, a composite measure of the relative abundances of the dominant generalist species and their feeding preferences, was positively related to observed herbivory rates. In contrast, estimated feeding pressure of orthopterans was not related to herbivory, although it was negatively related to LFT. This is plausible, as the majority of orthopterans collected in the plots were nymphs rather than adults, which may have been more readily influenced by mechanical defenses. Although all the species used in the calculation of estimated feeding pressure were confirmed generalist feeders, at no point over 2 yr was an orthopteran directly observed feeding on mature dipterocarp leaves in the field, while coleopterans were frequently observed. Orthopterans are therefore unlikely to cause large amounts of damage to mature leaves of these seedlings.

The estimate of community feeding pressure is a novel measure that seeks to determine whether the local composition of the insect community can be related to the amount of damage on a given species in a particular area. It assumes that preferences exhibited in laboratory feeding trials are transferable to field conditions and are an accurate reflection of the amount of feeding, and that herbivore species within taxa are equivalent in impact. This was reasonable for the four weevils, which were of comparable size, whereas the seven orthopterans varied in adult body size and also fed on foliage as nymphs. Community feeding pressure is also not weighted by absolute abundance of herbivores within a plot, which varies over time and according to environmental conditions. This study has shown that the measure may have value in interpreting the levels of herbivory caused by diverse insect herbivore communities by providing a simple composite variable to describe their effect. More studies are necessary to determine its potential usefulness.

By combining chemical and physical attributes of dipterocarp leaves and the insect communities that feed upon them, it appears that the most important factor driving the relationship between seedlings and their insect herbivores within this system was level of chemical defense (phenolic content). This forms the basis for interpreting the rates of damage on mature leaves, and may also be influencing the abundances and feeding preferences of the dominant generalist herbivores present on the seedlings. Although the study focused upon seedlings of only five species from one family of

tropical trees in a single location, it is clear that a limited number of simple measures were able to account for the bulk of the variation in rates of herbivory between these species.

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