Herbivory on planted dipterocarp seedlings in secondary logged forests and primary forests of Sabah, Malaysia

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ABSTRACT. Leaf defences, leaf nutritional quality and leaf expansion rates may vary with resource availabilities to plants. Such variation could affect rates of leaf loss to herbivores, particularly along the steep resource gradients in disturbed forests. Intraspecific and interspecific variation in leaf damage and leaf expansion rates were measured on dipterocarp seedlings planted into secondary forests 1, 5 and 15 y after logging, and in adjacent primary forest of Sabah, Malaysia. Herbivory rates or amounts of leaf damage were compared across habitats and species for expanding, recently expanded, and mature leaves of *Shorea leprosula* and *Dryobalanops lanceolata* (Dipterocarpaceae). In all four habitats, leaves of the faster growing *S. leprosula* sustained higher rates and amounts of leaf-area loss than did the tougher leaves of slower growing *D. lanceolata*. Expanding leaves accumulated more leaf-area loss per week than did mature leaves. In all habitats and in both species, more than 25% of expanding leaves disappeared entirely. Rates of leaf-area loss per week differed among habitats for expanding leaves but not for mature leaves. In a relatively open, 1-y-old logged forest, faster leaf expansion reduced the time leaves spent in the most vulnerable stage; however, in *S. leprosula* a greater rate of leaf area loss countered the shorter expansion time. Thus, leaves accumulated similar total damages across habitats, and herbivory did not produce differences among habitats in seedling growth or mortality. High levels of resources may increase both leaf palatability and leaf expansion rates, with counteracting effects on herbivory.

KEY WORDS: Danum Valley, dipterocarp, *Dryobalanops lanceolata*, herbivory rates, leaf damage, leaf expansion rates, logged tropical forests, secondary forests, *Shorea leprosula*

INTRODUCTION

In tropical forests, herbivores typically remove 10–30% of a plant's leaf area each year (Coley & Aide 1991, Coley & Barone 1996). To deter grazing by

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insects and mammals, plants deploy phenological, structural and chemical leaf defences. Although temporal and spatial variation is high (Aide & Zimmerman 1990, Coley 1983a, Lowman 1985), average rates of leaf loss to herbivores vary systematically among plant species and correlate with prevailing levels of leaf defences (Coley 1983b, 1986; Coley & Barone 1996, Lowman 1992b). Among-species differences in leaf defences and herbivory rates are related to resource availabilities in the typical habitats (Bazzaz *et al.* 1987, Coley *et al.* 1985). Despite the limited habitat tolerances of many plant species, conspecific individuals can experience a wide range of resource availabilities. For example, although many seedlings and saplings of persistent species tolerate the shaded conditions of the forest understorey, individuals that survive gap formation suddenly experience a high-light environment. Large differences in resource supply rates could result in differential leaf palatability, due to disparities in nutritional quality (especially nitrogen levels) and/or leaf defences, and thus differential herbivore attack.

Both interspecific and intraspecific patterns in leaf defences may relate to resource budgets (Bazzaz *et al.* 1987). Species adapted to resource-poor environments, such as deep shade, heavily defend their leaves, because these leaves are expensive to replace, and because the opportunity costs of defence are relatively low (Coley *et al.* 1985). Thus, understorey plants and seedlings of persistent species, tolerant of the low light conditions in the tropical forest understorey, tend to have more leaf defences and lower rates of herbivory than do forest gap and pioneer species, specialized for high light conditions resulting from disturbance (Coley 1983b, Coley & Aide 1991). In contrast, intraspecific patterns in leaf defences tend to be in the opposite direction from interspecific patterns (Bazzaz *et al.* 1987). Defensive investment increases in high resource environments, since particular resources, present in excess of amounts that can be directed toward growth, can be invested in leaf defences (Bryant *et al.* 1983, 1987; Davidson 1993). For example, where light is abundant relative to nitrogen, carbon might be invested in nitrogen-free defences such as tannins or terpenes. In environments with high levels of the usually limiting resource, plants could increase their defensive investment and thus reduce herbivory on their leaves (Bazzaz *et al.* 1987; Bryant *et al.* 1983, 1987). Species limited equally by light and nitrogen are thought to experience greater herbivory than those with excess carbon or nitrogen to invest in defensive function (Davidson 1993).

Young leaves are more vulnerable to herbivory than are mature leaves. In tropical forests, young expanding leaves suffer much greater rates of leaf-area loss to herbivores than do mature leaves (Coley & Aide 1991, Coley & Kursar 1996). Damage to young leaves may also be more important than indicated by the area removed, since damaged leaves may not grow to full size (Cooke *et al.* 1984). Young leaves are generally more nutritious to herbivores than are mature leaves (Kursar & Coley 1991, Stamp & Bowers 1990) and also have fewer structural defences (Kursar & Coley 1991). Toughness, a measure of

structural defences, tends to be negatively correlated with herbivory rates (Coley 1983b, Lowman 1992b, Lowman & Box 1983). Young leaves cannot develop maximum toughness until they have completed expansion (Kursar & Coley 1991), and leaf toughness increases dramatically about the time leaves stop expanding (Aide & Londoño 1989, Ernest 1989, Kursar & Coley 1991, Lowman 1992a).

Several strategies can reduce losses of young leaves to herbivores. Plants can reduce the palatability of young leaves, either by limiting their nutritional value or by producing chemical defences (Coley & Kursar 1996, Kursar & Coley 1991). Alternatively, plants can increase leaf expansion rates, thereby reducing the time during which leaves are especially vulnerable (Aide 1993). For example, *Gustavia superba* (Lecythidaceae) has very rapid leaf expansion, despite a large leaf size, and a specialist herbivore can successfully attack its young leaves only during a window of a few days (Aide & Londoño 1989). However, the two strategies of rapid expansion and low palatability appear to be physiologically incompatible (Coley & Kursar 1996, Kursar & Coley 1992). Rapid leaf expansion requires high enzyme concentrations (correlated with high nitrogen levels and high nutritional quality), particularly early in leaf expansion, and competition for resources prohibits simultaneous synthesis of secondary metabolites (Coley & Kursar 1996). Conversely, lower enzyme concentrations or increased investment in defensive compounds reduce leaf palatability, but also slow leaf construction and reduce the leaf expansion rate (Coley & Kursar 1996, Kursar & Coley 1992). As a consequence, very young leaves (5% of full size) of rapid expanders tend to be highly palatable (Aide & Londoño 1989, Kursar & Coley 1991), and species with rapid expansion tend to have higher rates of leaf damage than do those with slow expansion (Coley & Kursar 1996). Where leaf palatability cannot be further reduced, faster expansion may be both an ecological and an evolutionary response to decrease herbivory.

Leaf expansion rates, leaf chemical and structural defences, and nutritional quality of leaves all can vary across light environments. Within species, assuming approximately similar herbivore densities across habitats, herbivory rates may be more likely to vary among habitats with large differences in resource availability. In previously undisturbed forests, logging induces sudden and drastic changes in the light environment and microclimate. Openings are created in the forest canopy, significant soil disturbance occurs, and a large but heterogeneous amount of organic material is added to the soil (Nussbaum *et al*. 1995, Pinard & Putz 1996, Uhl *et al*. 1982). Although soil nutrient levels change very little, light levels increase substantially (Howlett 1998, Pinard & Putz 1996). Seedlings and saplings in logged sites experience a hotter and drier environment with higher light availability than do seedlings in the shaded and humid understorey (Howlett 1998, Turner & Newton 1990, Uhl *et al*. 1988). Since Southeast Asian dipterocarps (Dipterocarpaceae) tend to have high levels of carbon-based resins (Ashton 1982, Messer *et al*. 1990) and phenolics (Becker

1981, Waterman *et al.* 1988), they might be predicted to produce more leaf defences in logged forests than in primary forests. With more energy available, leaf expansion rates also could increase in logged forests. If either chemical defences or leaf expansion rates increase with light availability, plants in the recently logged forest should experience less herbivory than do their congeners in primary forest. Alternatively, enhanced photosynthetic capacity could increase leaf nitrogen levels in high light environments, and could thus lead to increased herbivory (Mooney & Gulmon 1982). Together with any habitat correlated herbivore abundances, interactions among these factors determine differences in leaf palatability and herbivory rates across habitat boundaries.

Along with implications for hypotheses concerning plant–herbivore interactions, among-habitat differences in herbivory rates could influence patterns of seedling growth and survival in logged forests. For two commercially valuable tropical tree species differing in shade tolerance, we compared leaf area losses to herbivores among four habitats that differed in light availability. In primary forest and three logged forest habitats of different ages, we assessed leaf expansion and herbivory rates on planted seedlings of *Shorea leprosula* Miq. and *Dryobalanops lanceolata* Burk. (Dipterocarpaceae). We monitored the expansion of new leaves and measured leaf area losses on expanding, young, and mature leaves.

<div align="center">METHODS</div>

Study site

We conducted this study at the Danum Valley Field Centre (DVFC) in Sabah, Malaysia. DVFC adjoins the 438-km^2 Danum Valley Conservation Area in the midst of a 10^6-ha forest concession reserved for timber production (Collins *et al.* 1991, Marsh & Greer 1992). The Sabah Foundation (Yayasan Sabah), a statutory body established by the Sabah legislature to sponsor economic development, manages both DVFC and the Conservation Area and operates the logging concession. Vegetation is primarily lowland dipterocarp forest (Newbery *et al.* 1992, 1996), dominated by emergent trees in the family Dipterocarpaceae. Since many of these canopy trees are commercially valuable, large areas of natural forest are managed for timber production. The terrain is rolling to steep and ranges from 200 to 1000-m elevation. Soils and geology are extremely variable, both locally and regionally (Acres *et al.* 1975, Marsh & Greer 1992, Nussbaum 1995). DVFC receives a mean annual rainfall of 2800 mm (Marsh & Greer 1992). Although all months average >100 mm of rainfall, two relatively dry periods occur in April and in August–September (Brown 1993, Marsh & Greer 1992). Daily temperatures reach a mean daily minimum of 22 °C with little seasonal fluctuation, while mean daily maxima range from 29 °C during December–February to 32 °C during the drier months of April and September (Brown 1993).

In December 1992, we selected three 16-m × 20-m plots in each of three

habitats: primary forest, and 5-y-old (Coupe 78) and 15-y-old (Coupe 88) pioneer-dominated secondary forests logged in 1978 and 1988. Primary forest plots were located in sites with no recent canopy gaps, and secondary forest plots had canopies dominated by *Macaranga* spp. (Euphorbiaceae) and relatively few understorey shrubs or saplings of primary forest species. In June 1993, three plots were established in a recently logged forest (Coupe 92, 1-y-old), which contained mixtures of pioneer seedlings and saplings, herbaceous weeds, and vines, and were expected to resemble the 5- and 15-y-old logged forests when they attain those ages. The site descriptions given here for logged forest plots applied only to portions of their respective coupes; sites of these types and sufficient size generally were found near roads and log yarding areas. In the secondary forests and the recently logged forest, following the standard practice for dipterocarp replanting projects, vines and herbaceous weeds were cut before planting. This site preparation reduced the canopy variation within habitat classes, and facilitated access for the experiments.

Study species

Each of the 12 plots was planted with seedlings of *Dryobalanops lanceolata* and *Shorea leprosula* (Dipterocarpaceae) as part of an experiment to assess potential growth rates in the four habitats described above (Howlett 1998). These locally common emergent species (Meijer & Wood 1964) are planted widely near DVFC in reforestation projects. Seedlings approximately 30-cm tall were acquired from the Yayasan Sabah/Face Project production nursery, where they had been cultivated from seeds under neutral density shading at 30% of full sunlight. Planting followed site selection and preparation in each habitat: in December 1992–February 1993 for primary forest, Coupe 78 and Coupe 88, and in June–July 1993 for Coupe 92. In each of the 12 plots, 40 seedlings of each species were planted at alternate positions in an 8 × 10 checkerboard array at 2-m spacing. In September 1993, the leaf area index (LAI), an indicator of canopy density above each plant, was measured with a LiCor LAI-2000 Plant Canopy Analyzer (Howlett 1998). Herbivory was monitored on 20 seedlings of each species, selected randomly from those surviving in each plot. Seedlings with neither a recently expanded young leaf nor an expanding leaf bud were rejected for this study.

Leaf damage measurements

Leaf area loss was measured on leaves of three age classes: (1) 465 mature leaves, during a 6-wk period, (2) 436 recently expanded leaves, at the time of full expansion and (3) 388 expanding leaves, from bud break through full expansion. During our initial visit to each seedling in the study, we marked a haphazardly selected mature leaf, measured a recently expanded leaf, and marked and measured the length of an expanding leaf bud. Some seedlings did not have leaves in all three age classes, so the sample sizes were unequal. At the start of the study, we estimated potential leaf areas (areas if leaves had

been completely intact) and herbivore damaged (missing) areas of the marked mature and recently expanded leaves. After 6 wk, we again measured the potential leaf areas and herbivore-damaged areas of the mature leaves. Every 2 wk, we measured the leaf lengths of expanding leaves and noted any missing leaves. We quantified potential leaf area and herbivore-damaged area of each expanding leaf when it had expanded completely, i.e. when a leaf had not changed length during 2 wk and had toughened to the condition of the recently expanded leaves when they were measured. Expansion times were calculated from the start of the first census interval during which a leaf bud at least doubled in length. Some leaves had expanded fully after 6 wk, but other leaves had not completed expansion after 10 wk, or the termination of the experiment.

All leaf area and leaf damage measurements were made in the field by enumerating filled squares in a transparent grid (Coley 1983b). Our data are presented as amounts of leaf damage (total per cent area losses of recently expanded and expanding leaves) or as herbivory rates (leaf damage per week for mature leaves during the 6-wk observation, and for expanding leaves during their expansion period). All mature leaves were observed for the same period, so accumulated damage and herbivory rates are equivalent. When leaf expansion times varied, herbivory rates on expanding leaves could show a different pattern than did total amounts of leaf damage to the same leaves.

Leaf toughness

Leaf toughness was measured for plants in a plantation habitat similar to the Coupe 92 site. We avoided damaging the plants that were the focus of the present study, because these plants were part of a longer-term experiment, and a number of them had few leaves. One recently expanded leaf and one mature leaf were collected from each of 12 plants of each species. Avoiding major veins, we used a Chatillon penetrometer (Chatillon Instruments, New York) to punch six holes in each leaf lamina. A leaf's toughness was defined as the mean force required to punch these six holes.

Statistics

All analyses were performed using the statistical package JMP 3.2 for Macintosh (SAS Institute 1994). Leaf toughness was compared between species and leaf-age categories with two-way ANOVA. For mature leaves, potential leaf areas were computed from the mean of initial and final size estimates. Within individual plants, amounts of damage to leaves of different ages were correlated with Kendall's τ, a nonparametric statistic. For each of the three sets of leaves, we used ANOVA to compare leaf damages and herbivory rates among species, habitats and plots nested within habitat. With plot nested within habitat, the replicate plots were treated as subjects, and the individual leaves were equivalent to multiple observations. Because amounts of leaf damage and herbivory rates were not normally distributed, we transformed herbivory rates and leaf damages by:

$$\log_{10} (1 + 1000 * (\text{proportion of leaf damaged}))$$

(see Coley 1983b). Missing mature and expanding leaves were excluded from ANOVAs. Because many of the other measurements were close to zero, inclusion of entire leaf losses would have distorted the distributions and rendered ANOVA inappropriate. In addition, missing mature leaves could have senesced and dropped naturally. LAI was included initially as a covariate in these models, and r^2-values and significance tests were compared between models with and without the covariate. Herbivory rates on mature leaves were contrasted to rates on expanding leaves with MANOVA. Mature-leaf herbivory rates and expanding-leaf herbivory rates, transformed as above, were the two dependent variables, and species, habitat, and plot-within-habitat were the independent variables.

Times to full expansion and times until complete loss to herbivores were compared among species and habitats with proportional hazards (Cox) survival models. Expanding leaves were considered to have left the experimental population when they were either completely lost to herbivores or fully expanded. Thus, 'time to event' was the same for both analyses, but leaves that were eaten were censored in the expansion model, and leaves that had fully expanded were censored in the leaf loss model. For leaf buds that did not change in size, expansion times were censored at 2 wk, the smallest interval in the study. The number of expanding leaves lost during expansion was compared among species and habitats with a three-way contingency table. In addition, numbers of leaves completing expansion during each of three time periods (4–6 wk, 6–8 wk and 8–10 wk) were compared by a contingency table test.

RESULTS

Leaf toughness

Mature leaves were significantly tougher than were recently-expanded leaves (F = 5, df = 1,44; P = 0.03), and *Dryobalanops* leaves were significantly tougher than were *Shorea* leaves (F = 509, df = 1,44; P < 0.0001). Mature *Dryobalanops* leaves were three times as tough as mature *Shorea* leaves (*Dryobalanops*: 347 ± 18 g [mean ± SE penetrometer pressure]; *Shorea*: 114 ± 6 g). Recently expanded *Dryobalanops* leaves were nearly as tough as were mature leaves (329 ± 8 g, or 95% of mature leaf toughness), while recently expanded *Shorea* leaves were much more tender than were mature leaves (84 ± 4 g, or 74% of mature leaf toughness); however, the leaf age by species interaction was not significant (F = 0.54, df = 1,44; P = 0.54).

Relationships among herbivory measurements

For mature leaves, the two estimates of potential leaf area were highly correlated (r = 0.98; n = 451, P < 0.0001), confirming the replicability of measurements. Initial and final leaf area estimates differed by a mean of just 4%. Only 17 marked mature leaves, or 4% of the total, were missing at the end of the 6-wk study. Numbers of mature leaves lost did not differ among species or habitats (three-way contingency table: χ^2 = 3.4, df = 4, P = 0.50).

Table 1. Results of analyses of variance comparing leaf damage and herbivory rates between two species of dipterocarp *Dryobalanops lanceolata* and *Shorea leprosula*, among forest habitats, and among plots nested within habitat.

	df	F	P
Recently-expanded leaf damage	15,420	7.1	< 0.0001
Model			
Species	1	81.2	< 0.0001
Habitat	3	1.2	0.31
Habitat*species	3	2.4	0.064
Plot[habitat]	8	1.8	0.069
Expanding-leaf damage	15,371	2.8	0.0004
Model			
Species	1	20.9	< 0.0001
Habitat	3	1.7	0.17
Habitat*species	3	1.5	0.22
Plot[habitat]	8	1.8	0.074
Expanding-leaf herbivory rate	15,264	4.9	< 0.0001
Model			
Species	1	42.6	< 0.0001
Habitat	3	2.8	0.041
Habitat*species	3	0.5	0.65
Plot[habitat]	8	1.9	0.061
Mature leaf herbivory rate	15,436	3.2	< 0.0001
Model			
Species	1	33.5	< 0.0001
Habitat	3	1.3	0.27
Habitat*species	3	2.7	0.044
Plot[habitat]	8	0.5	0.87
Mature leaf damage (incl. previous holes)	16,449	6.0	< 0.0001
Model			
Species	1	9.0	0.0028
Habitat	3	1.5	0.21
Habitat*species	3	0.8	0.52
Plot[habitat]	8	0.5	0.89
% holes	1	39.9	< 0.0001

Significant correlations occurred between herbivory rates on the same leaves during different time periods and between damage to different leaves of the same plants. Initial measurements of missing leaf area for mature leaves significantly predicted herbivory rates on those leaves during the observation period (Table 1). When pooled across both species and all habitats, the amounts of damage to expanding leaves were correlated with damage to recently expanded leaves of the same plants (Kendall's τ = 0.136, n = 362, P = 0.0004), but not with the herbivory rates on mature leaves. However, when calculated within species, this correlation was not significant for either species (*Shorea*: τ = 0.09, n = 180, P = 0.09; *Dryobalanops*: τ = 0.08, n = 182, P = 0.14).

Interspecific comparison

For all leaf age classes, herbivory rates and leaf damages differed significantly between species (Table 1). *Shorea* leaves sustained much more herbivore damage than did *Dryobalanops* leaves (Figure 1), losing three to five times as much leaf area to herbivory (Table 2).
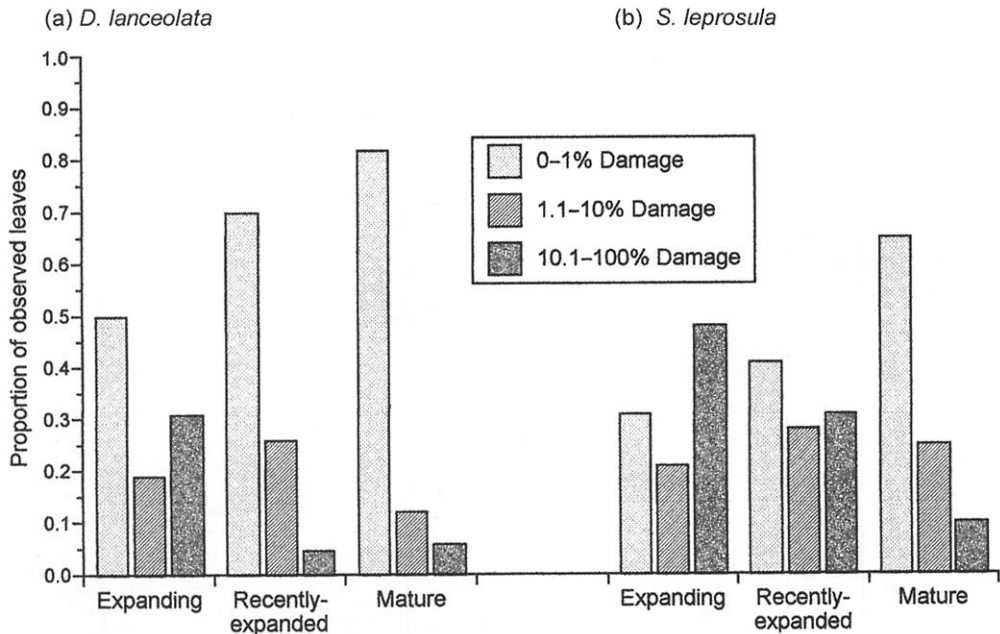
Figure 1. Observed leaf damage to seedlings of two dipterocarp species (a) *Dryobalanops lanceolata*, and (b) *Shorea leprosula*. For each of three age classes of leaves, vertical bars indicate the proportion of observations that fell into particular damage categories. Leaf damage did not differ significantly across the four habitats studied and are pooled across habitats.

Leaf damage and herbivory rates across habitats

Herbivory rates on mature leaves and amounts of damage to expanding and recently expanded leaves did not differ among habitats or plots (Tables 1 and 2). The habitat by species interaction was significant for herbivory rates on mature leaves but not for herbivory rates on expanding leaves or damages to expanding leaves and recently expanded leaves. After accounting for differences between species and among plots, herbivory rates to expanding leaves differed among habitats (Table 1). Least-squares mean herbivory rates were highest in Coupe 92, the most recently disturbed habitat, and lowest in Coupe 78; with values of 0.24, 0.16, 0.21 and 0.36% wk^{-1} in primary forest, Coupe 78, Coupe 88, and Coupe 91, respectively.

LAI differed among habitats, averaging 6.5, 5.1, 4.2 and 2.5 m^2 m^{-2} for primary forest, Coupe 78, Coupe 88 and Coupe 92, respectively (see also Howlett 1998). However, when LAI was included as a covariate in the models, it did not significantly predict leaf loss to herbivores for any of the leaf populations (P > 0.20).

Differences between young and mature leaves

In comparisons between herbivory rates on expanding and mature leaves, rates of leaf area loss were an order of magnitude less on mature leaves than on expanding leaves (MANOVA: F = 2.23, df = 15,194; P = 0.0068; Table 2).

Table 2. Mean leaf damage and herbivory rates for two species of dipterocarp seedlings, *Dryobalanops lanceolata* and *Shorea leprosula*, in four habitats.

Habitat	D. lanceolata				S. leprosula			
	Primary forest	Coupe 78	Coupe 88	Coupe 92	Primary forest	Coupe 78	Coupe 88	Coupe 92
Recently expanded leaf damage (%)[1]	2.80	3.78	1.91	1.41	15.2	18.9	8.14	11.2
Expanding leaf damage (%)[1]	2.43	0.67	2.03	1.82	9.05	11.1	12.9	16.3
Expanding leaf damage (%)[2]	34.9	24.0	33.5	24.2	52.3	34.1	34.3	39.4
Expanding leaf herbivory rate (% wk^{-1})	0.33	0.10	0.28	0.30	1.25	1.65	1.98	2.61
Mature leaf herbivory rate (% wk^{-1})	0.03	0.35	0.18	0.08	0.64	0.64	0.57	0.07

[1] does not include leaves entirely lost
[2] includes leaves entirely lost

Table 3. Expansion history of marked expanding leaves for two dipterocarp species, *Dryobalanops lanceolata* and *Shorea leprosula*, in four forest habitats

Habitat:	D. lanceolata				S. leprosula			
	Primary forest	Coupe 78	Coupe 88	Coupe 92	Primary forest	Coupe 78	Coupe 88	Coupe 92
Expansion history								
100% lost	11	11	19	13	10	15	14	17
Expanded in 6 wk	11	23	17	43	8	24	26	41
6–8 wk	11	16	16	0	3	13	16	1
8–10 wk	0	1	5	1	0	3	1	0
Expansion incomplete	4	2	3	0	2	0	1	0
Did not expand	20	6	0	3	28	5	2	1
Total number	57	59	60	60	51	60	60	60
Mean expansion time (weeks ± SE)	7.3 ± 0.2	6.9 ± 0.2	7.5 ± 0.2	6.3 ± 0.1	7.0 ± 0.3	6.9 ± 0.2	7.1 ± 0.2	6.2 ± 0.1

The contrast between herbivory rates on mature leaves and on expanding leaves differed among habitats (F = 6.18, df = 3,194; P = 0.0005), in that the three forested sites showed similar relationships between herbivory rates on mature leaves and expanding leaves, while plants in Coupe 92 sustained the highest herbivory rates on expanding leaves and the lowest herbivory rates on mature leaves. The two species showed similar patterns (F = 0.06, df = 1,194; P = 0.81), and the habitat by species interaction was not significant (F = 2.14, df = 3,194; P = 0.10).

Leaf expansion and entire leaf losses

Most of the losses of entire expanding leaves occurred at 2–4 wk, and loss functions did not differ significantly among habitats or between species (Cox-survival model: $\chi^2 = 3.2$, df = 7, P = 0.87). The 108 leaves entirely lost during expansion, 28% of all expanding leaves, represented similar proportions from both species and all habitats (Table 3; three-way contingency table: $\chi^2 = 4.6$, df = 7, P = 0.71).

Far fewer leaf buds expanded in the primary forest than in other habitats (Table 3; G-test: $\chi^2 = 101$, df = 3, P < 0.0001). Considering only those leaf buds that expanded, the proportion that reached full expansion during each time period differed significantly among habitats (G-test: $\chi^2 = 86.2$, df = 3, P < 0.0001) and generally decreased with increasing time since disturbance. In the multiway proportional-hazards model, times to full expansion differed among habitats ($\chi^2 = 22.5$, df = 3, P = 0.0001; Figure 2). Expansion rates were fastest in Coupe 92, where most leaves had completed expansion by 6 wk, and were slowest and most variable in the primary forest (Table 3). The maximum expansion rates were similar in all habitats, but most leaves in Coupe 92 expanded at the maximum rate, and progressively fewer did so in increasingly older forests. Times to full leaf expansion were similar for the two species ($\chi^2 = 0.9$, df = 1, P = 0.34). Since *Dryobalanops* leaves were nearly 20% larger on average than those of *Shorea* (one-way ANOVA: F = 72, df = 1,1150; P < 0.0001), but leaf expansion times were approximately equal, the leaf-doubling time must have been slightly longer for *Shorea* leaves.

DISCUSSION

Observed rates of leaf loss to herbivores can depend on a number of factors, including intrinsic defensive strategy, resource-mediated differences in leaf defences, nutritional quality, expansion rates and herbivore abundances and behaviours. For dipterocarp seedlings planted into primary forest and into successive stages of post-logging recovery, patterns in foliar herbivory agreed with trends already recognized for plant defences and herbivory in tropical forests. The effects of leaf age, habitat and species on variation in leaf herbivory are discussed below.
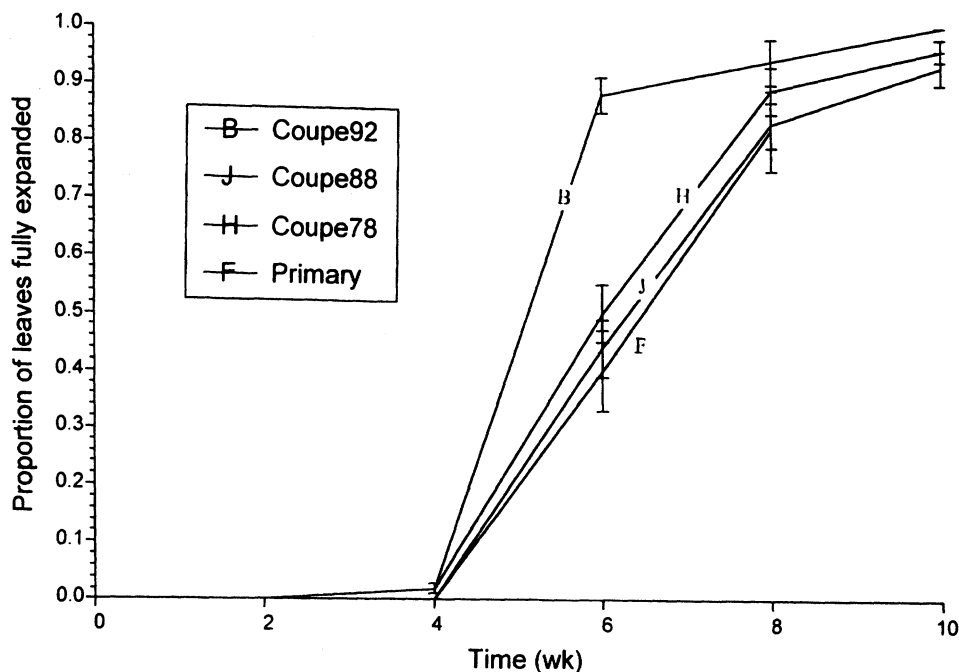
Figure 2. Proportion of marked leaf buds that reached full expansion, for expanding leaves of two diptero-carp species (*Dryobalanops lanceolata* and *Shorea leprosula*) combined. Vertical bars represent ± 1 SE.

Herbivory in relation to leaf age

Amounts of leaf damage and herbivory rates were higher on young leaves than on mature leaves (Figure 1, Table 2), consistent with patterns observed for other tropical trees (reviewed in Coley & Aide 1991, Coley & Barone 1996). For both dipterocarp species, rates of leaf-area loss were substantially greater on expanding leaves than on mature leaves, and they differed among habitats for expanding leaves but not for mature leaves (Table 1). Most herbivore damage accumulated during leaf expansion, and many potential leaves were entirely lost. A previous study also found similar accumulated damage on young and mature leaves of three dipterocarp species (Cooke *et al.* 1984), suggesting that most damage occurs during the expansion phase. This pattern likely results from the lower toughness and higher nutritional quality of expanding leaves (Coley & Kursar 1996). Although herbivory rates on expanding leaves differed among habitats, rates of entire leaf loss were similar in all habitats. This disparity suggests that entire leaf losses and leaf damage may have been caused by different agents. The high rate (28%) of leaf loss that we observed during leaf expansion was similar to the 27% losses found by Aide (1993) in Panama.

Although they are simple and fast, one-time damage measurements on recently expanded leaves did not account for leaves that were entirely lost to herbivores, and thus underestimated herbivory rates by up to 10 times. This is

a larger difference between expanding and mature leaf damage than has been found in other studies, where single measurements of leaf damage typically underestimate herbivory rates by two to five times (Coley & Barone 1996, Filip *et al.* 1995, Lowman 1985, 1992b).

Interspecific variation in herbivory rates

Shorea leprosula sustained higher rates of leaf area loss and more leaf damage than did *Dryobalanops lanceolata* (Figure 1, Table 2). *Dryobalanops* exhibited very low herbivory rates, particularly for mature leaves. These differences may be related to interspecific differences in defensive investment. Since *Shorea* grows significantly more rapidly than does *Dryobalanops* (Howlett 1998, Meijer & Wood 1964), the resource availability theory of plant defences (Coley *et al.* 1985) predicts that *Shorea* should invest less in leaf defence than does *Dryobalanops*. Consistent with this theory, both mature and recently expanded *Shorea* leaves were much less tough than were *Dryobalanops* leaves of comparable age, suggesting fewer structural defences. The between-species ratios of leaf toughness were very similar to the ratios of leaf damage, suggesting that these structural defences may have been important herbivore deterrents.

Intraspecific variation in herbivory

Light is one of the most limiting resources in the understorey of tropical forests, and differences in light availability could influence any light-dependent process. The two dipterocarp species in our study presumably rely on carbon-based structural or chemical defences, and thus individuals might be expected to increase their leaf defences in proportion to light availability across habitats, in the absence of systematic differences in soil fertility (Howlett 1998). Average canopy cover, inversely related to light availability, increased with time since logging and thus differed among the four study habitats (Howlett 1998), but the leaf area index (LAI) above individual plants was not correlated with differences in herbivory rates. There are at least two possible explanations for the failure of our LAI measurements to predict herbivory: (1) LAI measurements were taken above the plants and were not strongly related to the light environment experienced by individual leaves, some of which were shaded within the plant canopy, or (2) light environments had changed in the year between the LAI measurement and the herbivory monitoring. With these confounding factors and the high variability among plants in leaf losses to herbivores, it may be unrealistic to fit herbivory rates to a linear function of the overhead canopy.

Most life-time leaf damage occurs during the expansion phase (Coley & Kursar 1996), and damage to expanding leaves depends both on time until full expansion and on herbivory rates during this period. In the most open habitat in our study, leaves expanded more rapidly than in other habitats (Figure 2, Table 3), and very young leaves may have been more palatable as a result of increased concentrations of metabolic enzymes required for leaf growth (Coley & Kursar 1996, Kursar & Coley 1991). For *Shorea*, expanding leaves

were eaten at higher rates in the open, recently logged forest than in the primary forest understorey (Table 2). Other studies also have found higher rates of young leaf herbivory in sun than in shade, in part due to herbivore preferences for sun habitats (Basset 1991, Harrison 1987, Lincoln & Mooney 1984). However, faster leaf expansion offset higher herbivory rates in the most open habitat, with expanding *Shorea* leaves accumulating similar damage in all habitats. Faster expansion also benefited *Dryobalanops*, where leaves in the recently logged forest accumulated less damage than did leaves in the other habitats with similar herbivory rates. Similarly, for other species with light-limited rates of leaf expansion, faster expansion could reduce leaf damage in high-light habitats, even where increased palatability results in greater rates of leaf loss to herbivores.

Increased light availability may enhance both foliar tissue quality and leaf defences, with conflicting influences on herbivory rates. For example, sun leaves typically exhibit relatively high concentrations of nitrogen to support their high photosynthetic rates (Field & Mooney 1986, Mooney & Gulmon 1982), but they can also be better defended when mature (Denslow *et al.* 1990, Folgarait & Davidson 1994, Langenheim *et al.* 1981, Mole *et al.* 1988, Waterman *et al.* 1984). Considerable variation in whether sun or shade leaves are preferred by herbivores may depend in part on the relative scaling of nutritional quality versus foliar defences with light availability (Bryant *et al.* 1987, Denslow *et al.* 1990, Lincoln & Mooney 1984, Mooney & Gulmon 1982, Nichols-Orians 1991). At high leaf nitrogen levels, high photosynthetic capacities may help to recover some of the costs of carbon-based defences (Mooney & Gulmon 1982). The production of phenolics may be more sensitive to ratios of light to nutrients in fast-growing than in slow-growing species (Bryant *et al.* 1987), which could explain why, in the MANOVA results, mature leaf herbivory tended to decline with increasing light for *Shorea* but not for *Dryobalanops*. For *Shorea*, mature sun leaves may have been better defended than were mature shade leaves. However, without data for either leaf defences or leaf nutritional quality, relationships between these factors and herbivory remain tentative.

Factors such as herbivore population densities or behaviours, which are extrinsic to leaf tissue quality, could also be important in determining whether herbivory rates differ between sunny and shaded habitats. For example, high solar irradiance may enable insect herbivores to feed more rapidly or more efficiently, so that adults prefer to oviposit on leaves in the sun (Lincoln & Mooney 1984). Relatively rapid new leaf production in sunny habitats also may cause herbivores that specialize on young leaves to congregate in those habitats (Basset 1991). Thus, herbivore densities may vary among habitats. Preferences for sun versus shade leaves may differ among types of invertebrate herbivores (Basset 1991, Maiorana 1981), perhaps because herbivores experience different risks of predation in exposed and shaded sites (Maiorana 1981). However, for *Hybanthus prunifolius*, a tropical forest shrub, higher concentrations of herbivorous moths on gap plants than on plants in the shaded understorey were attributable to the higher tissue quality of leaves on gap plants, and not to higher

temperatures, or to the distribution of predators (Harrison 1987). Compre-
hensive studies such as Harrison's, which examined the relative influences of
a diversity of factors simultaneously, will be important in establishing any gen-
eral patterns of variation in herbivory over resource gradients.

Some individual plants may be more susceptible than others to herbivore
attack (Coley 1986). We observed that mature leaves with high previous herbi-
vore attacks experienced higher current rates of herbivory. Similarly, in Aus-
tralian temperate rain forests, Lowman (1992a) observed that leaves which
escaped herbivory when young were likely to remain largely damage-free until
senescence. Clark & Clark (1985) also found that damage rates were correlated
between observation periods (but see Coley 1983a). Consistent differences
among individuals could result either from genetic variation in resistance to
herbivory or from persistent environmental effects.

Effects of herbivory on growth and mortality rates

Leaf damage by herbivores was similar across light environments in the four
study habitats, and thus does not account for observed differences in seedling
growth and mortality rates (Howlett 1998). Further studies of the relationships
between leaf expansion rates and herbivory rates across resource gradients
might identify circumstances leading to different kinds of relationships
between these processes and seedling survival.

Modest rates of herbivory may have little effect on growth or mortality rates
of established seedlings of long-lived, shade-tolerant species. Previously, Becker
(1983) observed that even a one-time 25% leaf area removal did not increase
mortality of *Shorea leprosula* seedlings during a two-year study. Similarly, Coley
(1983a) found no correlation between short-term herbivory measurements and
plant growth rates for a set of Panamanian species, and Aide & Zimmerman
(1990) reported no relationship between herbivory rates and seedling sur-
vivorship in the liana *Connarus turczannowii* (Connaraceae). In contrast, in com-
paring individuals of *Piper arieanum* (Piperaceae) with low and high levels of
leaf damage, Marquis (1984) observed reduced growth rates in the latter group
even 2 y later. Clark & Clark (1985) found that herbivory on the first seedling
leaves of *Dipteryx panamensis* (Fabaceae) generally resulted in seedling death.
For seedlings of shade tolerant species, it may be that only serious defoliation
of small plants results in a dramatic increase in short-term mortality
(Nascimento & Hay 1994).

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