Seedling species determines rates of leaf herbivory in a Malaysian rain forest

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Abstract: Seedlings of five species in the Dipterocarpaceae were grown in experimental plots in Sabah, Malaysia. These were sited both in gaps and understorey and on alluvial and sandstone soils. Half of all seedlings were provided with a complete fertilizer. Herbivore damage levels were recorded on over 25 000 individual leaves in four surveys over the course of 2 y. Rates of herbivory were lower on mature leaves (0.07–0.8% leaf area mo^{-1} among species) than new leaves (2.1–4.4% leaf area mo^{-1}). There were no overall effects of light conditions, soil type, fertilizer treatment or time on rates of herbivory. The only consistent source of variation was that between species, with the three alluvial-specialist species suffering higher rates of damage than the two sandstone-specialists. Mature leaves of alluvial species received greater damage in sandstone soils, whereas sandstone species were damaged at equivalent rates on both soil types. New leaves were more damaged on their native soil type. Published herbivory rates vary in the timescales and methods of measurement. Nevertheless, the few comparable studies confirm that herbivory rates on seedlings in tropical rain forests are remarkably constant over time and across experimental treatments.

Key Words: Dipterocarpaceae, gap, habitat specialization, insect, reciprocal transplant, understorey

INTRODUCTION

Herbivory is one of the dominant interactions in tropical rain forests. Differential herbivory rates between species may influence their survival and growth, and therefore the regeneration of the forest as a whole, and can be responsible for habitat partitioning between tree species (Fine *et al.* 2004). It has been estimated that between 10% and 30% of tropical foliage is removed on an annual basis, with insects the principal defoliators (Coley & Barone 1996). Long-term monitoring of individual leaves is required to accurately determine these rates (Filip *et al.* 1995, Landsberg & Ohmart 1989, Lowman 1992). Young leaves suffer higher rates of damage than mature (Coley & Aide 1991, Coley & Barone 1996).

Herbivory rates vary between species. They are negatively correlated with leaf life span and with levels of anti-herbivore defences (Coley 1988, Coley & Aide 1991). Those species that have evolved to survive on nutrient-poor soils are expected to have longer leaf life span and higher levels of chemical defence, and therefore suffer lower herbivory rates (Coley *et al.* 1985). Environmental conditions also influence herbivory rates. Various authors have predicted herbivore damage levels to vary according to light environment (Aide & Zimmerman 1990) and leaf nitrogen concentration (Mattson 1980) which will be influenced by soil quality or fertilization, and season (Arnold & Asquith 2002). Reciprocal transplanting of species between soil types may also cause intraspecific variation in herbivory rates. For example, fast-growing plants accustomed to nutrient-rich soils may alter both their growth rates and their defensive investment when transferred to soils with a lower concentration of nutrients (Herms & Mattson 1992) and hence their susceptibility to herbivores.

Fine *et al.* (2004) demonstrated that a difference in the impact of herbivores on seedlings reciprocally transplanted across an edaphic boundary was a potential cause of habitat specialization among rain-forest trees, although rates of herbivory were not measured. Here we present the results from a reciprocal transplant experiment in which dipterocarp species of two ecological

specializations were grown in experimental plots in a rain forest in Sabah, Malaysia. The aim was to test established predictions that herbivory rates will vary with seedling species, leaf age, soil type, nutrient availability and light availability. In contrast to many previous studies which measure standing levels of herbivory, here we record damage levels on individually marked leaves over a 2-y period to estimate true herbivory rates.

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 reserve contains two principal types of mature mixed dipterocarp forest. These are defined edaphically and differ in structure and species composition. Alluvial soils 15–30 m asl are dominated by canopy trees of *Parashorea tomentella*, *Shorea johorensis* (Dipterocarpaceae) and *Eusideroxylon zwageri* (Lauraceae). This is interspersed with ridges of sandstone-derived soils up to 337 m, with forests dominated by *Shorea multiflora*, *S. beccariana* and *Dipterocarpus acutangulus* (Dipterocarpaceae). Small pockets of kerangas (heath) forest also occur. Full descriptions can be found in Fox (1973); nomenclature follows Ashton (1982).

Species studied

Five species of dipterocarp were grown in the experiment; *Hopea nervosa*, *Parashorea tomentella*, *Shorea fallax*, *S. multiflora* and *H. beccariana*. Their ecological characteristics and details of collection are summarized in Table 1. All are climax species rather than pioneers (*sensu* Swaine & Whitmore 1988), in that they are capable of germination, establishment and survival beneath the forest canopy. Three of the species are restricted to alluvial soils and two to sandstone. The species were chosen to test the effect of habitat specialization on their responses

Table 1. Characteristics of dipterocarp seedling species. Abundance refers to the relative natural abundance of the species within the Sepilok reserve as recorded by R. Nilus (unpubl. data) and by personal observation.

Species	Soil type	Abundance	Collection	Year
Hopea nervosa	Alluvial	Low	Danum Valley	1997
Parashorea tomentella	Alluvial	Very high	Danum Valley	1996
Shorea fallax	Alluvial	Absent	Danum Valley	1998
Shorea multiflora	Sandstone	Very high	Sepilok	2000
Hopea beccariana	Sandstone	High	Sepilok	2000

to different environmental conditions. Seedlings of the three alluvial species were collected from Danum Valley during mast fruitings in various years (Table 1), potted in 5 × 20-cm bags, and stored under 30% shade cloth in the FACE (Forests Absorbing Carbon Emissions) project nursery until January 2000. They were transferred to the Forest Research Centre nursery and stored beneath two layers of 80% shade cloth from January to March 2000. Seedlings of the two sandstone species were collected from the understorey in Sepilok from March to May 2000.

Experimental design

The experiment incorporated 10 sites, five located in alluvial lowland forest and five on sandstone ridges. Each site comprised a gap plot and paired understorey plot no more than 50 m from the gap edge. Natural tree-fall gaps from 400–600 m² were utilized. The remains of trunks and branches were removed, along with all plants above 50 cm in height. In one gap plot overhanging branches were removed from neighbouring trees. Each paired understorey plot had approximately the same aspect and slope as the gap. No clearing of the understorey or other pre-treatment took place.

Seedling heights (greatest distance from base to growing tip) were used as the basis for allocation into the plots using a randomized block design to ensure an even distribution of seedling species within the plot with respect to potential microclimatic gradients. Each block of 10 seedlings contained two seedlings of each species, with and without fertilizer (see below), randomly ordered within the block. There were 15 blocks per plot. An initial ANOVA confirmed that there were no significant differences in seedling lengths between the sites or treatment groups. Planting took place in March 2000. Seedlings were planted in a grid pattern, 75 cm apart, and at least 1.5 m from the gap edges. Paired understorey plots matched the shapes of the gap plots. In the understorey plots, seedlings were given a leeway of 50 cm to avoid planting directly beneath another plant. Seedlings were uniquely numbered with a metal tag tied to the base.

Seedlings were watered immediately after planting and on every day with no significant rainfall for the next 3 mo. Despite this, there was a high mortality of seedlings in the gaps caused by an exceptional drought during April. Dead seedlings were replaced continuously until June 2000 using seedlings of identical height from the Sepilok nursery wherever possible. A further collection of wild seedlings took place, which were planted as replacements at the end of June, once they had fully acclimatized to gap conditions. All mortality after the end of June 2000 was considered to be due to experimental treatments and no further replacement or watering took place. Gap plots were periodically cleared of competing vegetation.

Fertiliser was applied biannually (10–12 August 2000, 4–8 March 2001, 25–29 September 2001, 9–13 March 2002) using Agroblen (SCOTTS) slow-release complete fertilizer (16N : 8P : 9K : 3Mg + trace elements). A narrow trench was dug around each seedling (*c.* 5 cm depth and 5 cm from the base), into which 12 g of fertilizer was spread before replacing the soil. All seedlings were trenched and the soil replaced to control for potential root damage during fertilization.

Herbivory assessment

The herbivory surveys began 4 mo after planting. A structured random subsample of the seedlings within the experiment was chosen, excluding replacements planted later than March 2000. There were five replicates of each species and fertilizer treatment per plot (1000 seedlings overall). For the first survey leaves were sampled from the second highest branch with secondary thickening upwards. For seedlings without branches all stem leaves were sampled from the base. A minimum of four mature leaves were surveyed per seedling. Leaves were numbered using an indelible marker pen, close to the midrib and *c.* 1 cm from the petiole. Senescent or heavily damaged leaves (mechanical or fungal) were excluded. Repeat surveys typically added two new branches – the highest new branch with secondary thickening and a second branch halfway through the new growth. New leaves from growth on previously surveyed branches were also added. A minimum of five new leaves per gap plant were added in each survey; in practice this was usually many more. Each survey took approximately 2 mo.

Four complete herbivory surveys were conducted over 2 y (June–August 2000, February–March 2001, September–October 2001, April–May 2002). During later surveys death or abscission reduced the number of leaves on many understorey seedlings, and therefore new plants were included to replace them, although measurements continued on any remaining marked leaves on the original seedlings. In understorey plots where five seedlings with four or more leaves could not be found, every available leaf was sampled.

Herbivory was scored using a practised estimate of lamina damage based on percentage classes (0%, < 2%, 2–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–100%). Accuracy of estimates was confirmed on a subsample of leaves from each species using a grid scale. Alluvial Plot 1 was initially surveyed twice to check the replicability of the estimates; in over 99% of cases leaves received identical scores in both counts. Further checks of repeatability took place in subsequent surveys. Damage was defined as removal of potential photosynthetic tissue, and as such included leaves rolled or sewn together, even if not entirely consumed by herbivores. Where damage

during development had disfigured a leaf, its potential leaf area was considered to be the same as its closest neighbouring entire leaves, and the total damage to be the difference between its potential and actual leaf area. Absent leaves were not included as herbivory unless the petiole was still attached. It was seldom possible to determine the cause of abscission, as it was often the result of natural senescence due to age, fungal infection, mechanical damage or drought.

A total of 45 238 damage estimates were made over four surveys from a total of 25 749 individual leaves, of which 7132 were present in the first survey, the remainder being added in subsequent surveys. Rate calculations used the first survey as the baseline.

Statistical analysis

Leaves were split into two categories: mature (resurveyed) and new (surveyed for the first time). Replication for all analyses was considered to be at the plot level. A plot sample for any given species and treatment was used only if there were data from at least five new leaves from three different plants. The scarcity of new leaves on some species in the understorey (especially *P. tomentella* and *S. fallax*) necessitated this. In practice, 94% of samples contained at least 10 new leaves, and 92% recorded new leaves from at least four plants.

Rates of herbivory on mature leaves were calculated from the difference in damage levels on individual leaves between surveys using the mid-points of the percentage damage classes and means calculated for each plot. In a small number of cases, subsequent surveys on a particular leaf recorded a lower estimate of herbivory. This was an artefact caused by secondary infection, leaf dieback or mechanical damage. Apparently negative rates of herbivory represent sampling error and were included in the calculations. To standardize rates between surveys, the increase in damage was divided by the number of months (to the nearest half month) between surveys on each individual plot. For new leaves the average rate of herbivory was assumed to be equal to the recorded proportion of damage in a given survey divided by half the number of months since the previous survey to account for their continuous production. This assumes both an even rate of growth and of herbivory between surveys.

Data were arcsine-transformed prior to analysis. A small increment ($\delta = 0.015$) was added to the herbivory rates on mature leaves to permit transformation. Analysis followed the GLM procedure in SPSS v.12.0.1 using a design incorporating all relevant interactions (Appendices 1 and 2). A post-hoc contrast of species adapted to each soil type was included.
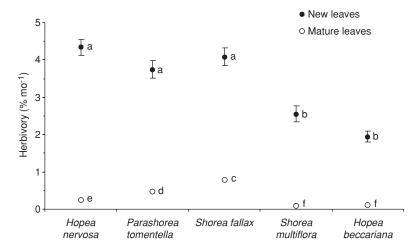
Figure 1. Rates of herbivory on mature and new leaves of seedlings of five species of dipterocarp. Data combined across all treatments. Mean $\pm$ 1 SE. Bars with different letters are significantly different (Duncan's Mean Multiple Comparison, $\alpha < 0.05$).

RESULTS

Mature leaf herbivory rates were an order of magnitude lower than for new leaves ($F_{1,436} = 300$, $P < 0.001$) (Figure 1). Mature leaves of sandstone specialists *S. multiflora* and *H. beccariana* lost 0.08% and 0.11% of leaf area mo^{-1} respectively, whereas the highest rates (0.79% mo^{-1}) occurred on *S. fallax*. For new leaves the rate ranged from 1.94% on *H. beccariana* to 4.34% leaf area mo^{-1} on *H. nervosa*, contrasting with only 0.24% mo^{-1} on its mature leaves.

Mature leaves

There were highly significant differences in the rates of herbivory on mature leaves of seedlings of the five species ($F_{4,546} = 41.3$, $P < 0.001$). The three alluvial-specialist species (*S. fallax*, *P. tometella*, *H. nervosa*) suffered greater rates of herbivory than the sandstone-specialists (*S. multiflora*, *H. beccariana*) (Figure 1). There were no significant effects of light environment ($F_{1,8} = 0.001$, $P = 0.974$), soil type ($F_{1,8} = 1.63$, $P = 0.238$) or fertilizer treatment on the rates of herbivory ($F_{1,546} = 0.528$, $P = 0.468$), nor was there any variation in rates of herbivory between the three survey intervals ($F_{2,546} = 0.663$, $P = 0.516$).

A significant interaction between species and soil type occurred ($F_{4,546} = 6.69$, $P < 0.001$). The three species native to the alluvial forest were damaged at a greater rate when planted on sandstone soils, while the species native to the sandstone forest were damaged at an equivalent rate in both soil types (Table 2). An interaction between light environment and plot nested

Table 2. Rates of herbivory on mature and new leaves of dipterocarp seedlings specialized to alluvial or sandstone soils when grown on both soil types in a reciprocal transplant experiment. Mean $\pm$ 1 SE. Post-hoc comparisons within classes of leaves were conducted as part of a larger analysis (see text). Means with different letters within leaf-age classes are significantly different (Duncan's Mean Multiple Comparison, $\alpha < 0.05$).

Soil type	Species affinity	n	Herbivory (% mo^{-1})
Mature leaves			
Alluvial	Alluvial	3	0.32 ± 0.04^b
	Sandstone	2	0.10 ± 0.03^c
Sandstone	Alluvial	3	0.56 ± 0.05^a
	Sandstone	2	0.06 ± 0.02^c
New leaves			
Alluvial	Alluvial	3	4.80 ± 0.26^a
	Sandstone	2	1.96 ± 0.22^d
Sandstone	Alluvial	3	3.45 ± 0.23^b
	Sandstone	2	2.56 ± 0.25^c

within soil type ($F_{8,546} = 3.39$, $P = 0.001$) indicates that the differences between gap and understorey were variable between sites. No other significant interactions occurred (see Appendix 1 for the full GLM table).

New leaves

There was significant variation in rates of herbivory on new leaves between the five species ($F_{4,436} = 29.5$, $P < 0.001$). Again, the three alluvial species suffered higher rates of herbivory than the two sandstone species (Figure 1). As with the rates of herbivory on mature leaves, there was an interaction between species and soil ($F_{4,436} = 8.19$, $P < 0.001$). In contrast to the mature

leaves, rates of herbivory were greatest on new leaves in their native soil type (Table 2).

Once again the rates of herbivory overall were not influenced by light environment ($F_{1,8} = 0.188$, P = 0.675), soil type ($F_{1,8} = 0.765$, P = 0.406) or fertilizer treatment ($F_{1,436} = 1.46$, P = 0.227). An interaction between species and light occurred ($F_{4,436} = 5.46$, P < 0.001), due to greater rates of herbivory on *P. tomentella* and *H. beccariana* in the gaps and *H. nervosa* and *S. fallax* in the understorey. There were no other significant interactions (see Appendix 2 for the full GLM table). There was however variation between the three survey intervals ($F_{2,436} = 11.8$, P < 0.001). This was due to an increase in herbivory on new leaves of *H. nervosa*, *P. tomentella* and *S. multiflora* between the first and second survey intervals; the rates thereafter remained constant.

DISCUSSION

Rates of herbivory were largely constant over the 2 y of the study. There were no overall differences in rates between gap and understorey habitats, alluvial and sandstone soils, or fertilized and unfertilized seedlings. The only consistent differences in rates of herbivory on both mature and new leaves were between species. This initially seems a surprising finding, since a wealth of literature on tropical herbivory has reported great variability in the levels of herbivory on the leaves of tropical tree seedlings between different species and environmental conditions. However, the majority of these studies have inferred rates of damage from standing levels (for example: Blundell & Peart 1998, Campo & Dirzo 2003, Filip *et al.* 1995, Landsberg & Ohmart 1989, Lowman 1992, Marquis *et al.* 2001, Newbery & de Foresta 1985, Williams-Linera & Herrera 2003).

Single measurements of standing damage have been shown to misrepresent true patterns of herbivory (Newbery & de Foresta 1985). This has led to conflicting predictions about the impact of environmental factors on rates of herbivory. For example, Coley & Barone (1996) reached the conclusion, primarily based upon standing damage measures, that understorey leaves receive a greater amount of herbivory than those in the canopy. In contrast, others have claimed herbivory to be greater within gaps than the understorey (Lincoln & Mooney 1984, Whitmore & Brown 1996). In the present study the rates of herbivory were identical beneath and outside the canopy.

There have been relatively few extensive surveys of rates of herbivory which compare across habitats, treatments or seasons published in the literature, but those that have also found no significant differences in herbivory rates in relation to environmental factors. Howlett & Davidson (2001) recorded rates of foliar herbivory on mature leaves of dipterocarp seedlings and found no variation between closed-canopy primary forest and secondary forests of various ages. Aide & Zimmerman (1990) recorded no differences in mature leaf herbivory rate across a continuum of light environments on a neotropical liana. Coley (1983a) demonstrated equivalent rates of herbivory between gap and understorey habitats on a range of species. Other studies have found little variation in rates of herbivory on developing leaves across environmental conditions. Angulo-Sandoval & Aide (2000) followed tagged leaves on seedlings in Puerto Rico throughout their development, and found no variation in their rates of herbivory between pronounced wet and dry seasons. In the study by Howlett & Davidson (2001), although rates did vary between forest types, no clear pattern emerged.

If, as our results suggest, the species of a seedling is the principal factor in determining the rates of herbivory suffered, this has profound implications for our understanding of the role of herbivory in competitive interactions between rain-forest tree seedlings. The lack of a consistent difference between light environments, soil types and nutritional status suggests we cannot make gross inferences about the intensity of herbivory in different areas. Nevertheless, the selective pressure imposed by herbivores may still depend upon the individual circumstances of any particular seedling. For example, since seedlings in the understorey may only receive 1–2% of full daylight (Chazdon 1986), the impact of a given amount of foliar herbivory will be greater beneath the canopy (Coley 1983b).

Rates of herbivory were an order of magnitude greater on new leaves relative to mature (Figure 1). This is a common finding, reflecting the greater palatability of young leaves to insect herbivores (Coley 1980, Coley & Aide 1991, Coley & Barone 1996). It is likely that the rate of damage to new leaves has been underestimated, by a factor of 2–5 if abscised leaves are considered to have been entirely eaten (Aide 1993, Coley & Barone 1996, Lowman 1992), although this is a debatable assumption. The rates showed a greater degree of variability than was evident for mature leaves, which may reflect the greater degree of error in the calculations due to reduced replication, especially in the understorey and sandstone plots, and because of the dual assumptions of even growth and herbivory upon which the estimates were based.

Species adapted to nutrient-poor soils are expected to have longer leaf life span, higher levels of chemical defence, and therefore receive lower rates of damage (Coley *et al.* 1985). In the present study, species characteristic of the less-fertile sandstone soils suffered lower rates of herbivory on both mature and new leaves (Figure 1).

The response of habitat specialists to reciprocal transplantation is a source of considerable interest in the light of recent evidence that herbivores may be

responsible for community partitioning between soil types in Amazonian forests (Fine *et al.* 2004). The present study found conflicting evidence for this, at least in terms of our measures of rates of herbivory. Mature leaves of species characteristic of alluvial soils were indeed damaged at a greater rate when grown in the sandstone forest, although sandstone species were damaged at equivalent rates on both soils. In contrast, the rates of herbivory on new leaves imply a greater rate of herbivory on the native soil types of the two groups (Table 2).

The present study has recorded rates of herbivory on more than 25 000 leaves over 2 y, representing a larger body of data than has been published elsewhere to date. Nevertheless, it incorporated only five species within a single family of tropical trees, and it is not known how general these results may be. The five species may have varied in their adaptation to environmental conditions, particularly light availability. The significant interaction in new leaf herbivory rates between species and light treatments hints at this, although a similar result was not found for the mature leaves. There is a need for more studies to determine the extent to which rates of leaf herbivory are a factor in habitat partitioning between species, and the impact of these rates on the growth and survival of seedlings.

ACKNOWLEDGEMENTS

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Appendix A. Results of GLM analysis comparing mean rates over time of herbivory on mature leaves between five species of dipterocarp among soil types (alluvial and sandstone), light habitat (gap and understorey), fertilized or unfertilized, and among plots nested within soil type.

	df	F	P
Model	1	6773	< 0.001
Species	4	41.3	< 0.001
Soil	1	1.63	0.238
Light	1	0.001	0.974
Fertilizer	1	0.528	0.468
Interval	2	0.663	0.516
Species × soil	4	6.69	< 0.001
Soil × light	1	1.44	0.264
Soil × fertilizer	1	0.320	0.572
Plot × light (soil)	8	3.39	0.001
Plot (soil)	8	1.40	0.322
Species × light	4	1.83	0.121
Light × fertilizer	1	0.227	0.634
Species × fertilizer	4	0.910	0.458
Species × soil × light	4	2.06	0.085
Soil × light × fertilizer	1	1.45	0.229
Species × soil × fertilizer	4	0.394	0.813
Species × light × fertilizer	4	0.158	0.959

Appendix B. Results of GLM analysis comparing mean rates over time of herbivory on new leaves between five species of dipterocarp among soil types (alluvial and sandstone), light habitat (gap and understorey), fertilized or unfertilized, and among plots nested within soil type.

	df	F	P
Model	1	2325	< 0.001
Species	4	29.5	< 0.001
Soil	1	0.765	0.406
Light	1	0.188	0.675
Fertilizer	1	1.461	0.227
Interval	2	11.8	< 0.001
Species × soil	4	8.19	< 0.001
Soil × light	1	1.61	0.239
Soil × fertilizer	1	0.647	0.422
Plot × light (soil)	8	2.77	< 0.001
Plot (soil)	8	0.732	0.665
Species × light	4	5.46	< 0.001
Light × fertilizer	1	0.196	0.658
Species × fertilizer	4	1.52	0.195
Species × soil × light	4	1.18	0.319
Soil × light × fertilizer	1	0.283	0.595
Species × soil × fertilizer	4	0.664	0.617
Species × light × fertilizer	4	0.642	0.632