

Canopy cover mediates interactions between a specialist caterpillar and seedlings of a neotropical tree

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Summary

1. Light availability may be crucial for understanding dynamics of plant–herbivore interactions in temperate and tropical forest communities. This is because local light availability can influence both tree seedling tolerance and susceptibility to herbivory – yet how they mediate levels of insect herbivory that vary with the density of host population is virtually unknown. Here we tested predictions of three key, non-mutually exclusive hypotheses of plant–herbivore interactions: the Limiting Resource Model (LRM), the Plant Vigour Hypothesis (PVH), and the Janzen–Connell Mechanism (JCM).

2. In an Amazonian forest, we planted *Swietenia macrophylla* seedlings (c. 5 months old) into natural canopy gaps and the shaded understorey and simulated the damage patterns of the specialist herbivore moth, *Steniscadia poliophaea*, by clipping seedling leaves. Over the next 8 months, we monitored seedling performance in terms of growth and survivorship and also quantified herbivory to new young leaves on a seasonal basis.

3. In support of the LRM, severe leaf damage ($\geq 50\%$) was lethal for *Swietenia macrophylla* seedlings in the understorey, but in gaps only reduced seedling growth. In support of the PVH, gap seedlings suffered greater post-simulated herbivory (up to 100% defoliation) by *S. poliophaea* caterpillars than their understorey counterparts.

4. Adding a novel dimension to the Janzen–Connell hypothesis, we found that early wet season herbivory of seedlings in gaps increased with conspecific adult density within a 125-m radius; whereas in the understorey only those seedlings within 50 m of a *Swietenia* tree were attacked by caterpillars.

5. *Synthesis.* These results suggest lepidopterans that need young leaves for food may forage more widely in forests to find seedlings in light-rich canopy gaps. Moths may achieve this successfully by being first attracted to gaps, and then searching within them for suitable hosts. A conceptual model, integrating conspecific adult tree density with light-driven changes in seedling tolerance/vigour and their susceptibility to herbivory and mortality, is presented. Spatial variation in the light available to tree seedlings often affects their tolerance and vigour, which may have important consequences for leaf-chewing insects and the scale of density-dependent herbivory in forests.

Key-words: Amazon forest, big-leaf mahogany, caterpillar herbivory, density-dependent folivory, Janzen–Connell, light gaps, Limiting Resource Model, Plant Vigour Hypothesis, seedling growth and mortality, *Swietenia macrophylla*

Introduction

Despite the ubiquity of leaf-chewing insects in species-rich forests and the potential vulnerability of tree seedlings to their predations, few studies have examined the impacts of insect

folivores on seedling growth and mortality (Becker 1983; Massey *et al.* 2005). Even fewer studies have explored the way seedling herbivory is jointly influenced by additional biotic and abiotic factors (Coley & Barone 1996; Swaine 1996; but see recently Pearson *et al.* 2003; Chacón & Armesto 2006; Massey *et al.* 2006). Local light availability may be critical to understanding the dynamics of plant–herbivore interactions in forest communities, especially in the tropics where light is the most limiting resource for plant growth (Chazdon *et al.*

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1996). In these forests, treefalls create openings or 'gaps' in the canopy that increase light transmission to the ground and cue the regeneration of most tree species (Hartshorn 1978; Baker & Bunyavejchewin 2006). Hence, under the Limiting Resource Model (LRM), the impact of herbivore attack on plant fitness should increase under conditions of limited carbon availability (i.e. shaded understorey) because of direct interference with the plant's capacity to capture precious light (Wise & Abrahamson 2005). In other words, folivory worsens an already major resource limitation faced by tropical tree seedlings. Indeed, several aspects of tree juvenile performance were found to be compromised under low- compared to high-light environments for both mammalian (e.g. Howe 1990; Osunkoya *et al.* 1993) and insect herbivory (e.g. Blundell & Peart 2001; Sullivan 2003).

By contrast, the Plant Vigour Hypothesis (PVH) explains how local resource availability modifies the physical condition of plants, which in turn may determine the amount of herbivory they experience. Specifically, the PVH predicts that herbivores will target faster growing plants and/or relatively large plant parts because they are more nutritious and promote larval success (Price 1991). Young leaves are good food because they are soft and rich in nitrogen and water, yet poorly defended mechanically against insect herbivores due to biophysical constraints (Coley & Barone 1996; Swaine 1996). Therefore, the PVH should apply especially to insects whose larval development requires young, expanding plant tissues, and hence might be adversely affected by stressed plants in the unproductive understorey. By contrast, light gaps promote vigorous growth in tree seedlings accompanied by the production of young leaves: the major resource for insect folivores (Popma & Bongers 1988; Coley & Barone 1996; Basset *et al.* 2001). The damage caused to young leaves is not trivial because of their high photosynthetic rates, nitrogen content, future photosynthetic contribution to the seedling's energy balance, and the fact that they are more likely to be lost than mature leaves when damaged (Blundell & Peart 2000).

Patterns of plant tolerance (LRM) and defence (PVH) and, as a consequence, impacts of insect folivory on young leaves of seedlings, should thus vary spatially due to resource heterogeneity created by these dynamic gap formations (Coley 1993; Massey *et al.* 2005). Yet, no differences in herbivory to young leaves were observed between light gaps and understorey juveniles for either *Trichilia cipo* in Panama or *Shorea quadricornis* in Borneo (Coley 1983; Blundell & Peart 2001). In Malaysia, seedling defoliation was lower in forest gap-centres than gap-edges in five dipterocarp species, suggesting herbivory is less prevalent in high-light environments (Massey *et al.* 2005). In Panama, seedlings of three neotropical pioneer tree species lost, on average, more leaf area in larger vs. smaller sized gaps (Pearson *et al.* 2003). In the same forest, a specialist moth (*Zunacetha annulata*) attacked *Hybanthus prunifolius* shrubs in gaps because of enhanced foliage quality provided to larvae, despite a greater risk of predation (Harrison 1987).

These two hypotheses (LRM and PVH) further suggest that spatial variation in light availability – and thus potential food availability for herbivores – created by gaps may modulate

another spatially explicit biotic interaction: that between leaf herbivory and the density of host plants. Specialized herbivores can alter tree distributions in forests by attacking conspecific seedlings and saplings where their densities are greatest (in particular, near parent trees), thereby suppressing species that may otherwise be competitively superior (Janzen 1970; Connell 1971). If these herbivores remain highly localized (i.e. beneath tree crowns) however, they will do a poor job of promoting coexistence unless they, or some other agent(s), also target more seedlings and saplings at increasing densities of conspecific tree adults (Schupp 1992) – that is, where parent clustering leads to potential clusters of hosts via overlapping seed inputs (Webb & Peart 1999; see Fig. 9 in Janzen 1970). However, the scale on which this happens in tropical forests is poorly understood, despite increasing recognition that many ecological processes are scale-specific and that density dependence can occur at multiple spatial scales in plant populations (Schupp 1992; Gunton & Kunin 2007). The underlying mechanism of the Janzen–Connell model (JCM) assumes: (i) herbivores have fairly narrow diet ranges, (ii) they can find and eventually kill tree juveniles, and/or retard their growth and recruitment into larger size-classes, and (iii) the dispersal distance needed to escape from herbivores is unaffected by canopy disturbances. At the same time, however, the LRM and PVH suggest that light gaps should influence both the tolerance and susceptibility of young trees to herbivores – with the net implications for JCM still unclear (Hammond & Brown 1998). Several studies have quantified seedling/sapling performance and attendant insect herbivory under JCM (e.g. Clark & Clark 1985; Blundell & Peart 1998), although only two studies have at the same time addressed the influence of light availability (Angulo-Sandoval & Aide 2000; Sullivan 2003). Neither study found evidence to suggest that light availability influenced the relationship between the degree of herbivory and conspecific densities.

Here, we report on a field experiment designed to simultaneously test key predictions of LRM, PVH and JCM. We studied a natural population of a long-lived tropical tree, *Swietenia macrophylla* King (Meliaceae); also known by its common name, 'big-leaf mahogany'. This species is interesting not only because of its high economic value and endangered status (Grogan & Barreto 2005), but also because of proposed density-dependent herbivory on young leaves of its seedlings by a putative specialist caterpillar, *Steniscadia poliophaea* (Grogan 2001; Grogan & Galvão 2006; Norghauer *et al.* 2006a). We predicted that: (i) seedlings would tolerate simulated herbivory from leaf clipping better in gaps than in the understorey with respect to survival (LRM); (ii) these clipped seedlings would be less acceptable than controls to the specialist herbivore due to decreased plant vigour and/or possible induced resistance (PVH); (iii) because of potentially greater biomass produced by plants in gaps, seedlings there would suffer more damage to new leaves by the specialist folivore than in the understorey (PVH); and (iv) differences in canopy cover (i.e. productivity) would lead to differences in the spatial scale of density-dependent herbivory of the young leaves of seedlings (JCM).

Methods

STUDY SITE

Research was conducted at the Kayapó Centre for Ecological Studies (Pinkaiti), a station and forest reserve located in the Kayapó Indigenous Area (KIA) in south-east Pará, Brazil (7°46'14" S, 51°57'43" W). This 8000-ha reserve has an unlogged population of *S. macrophylla* surrounded by a huge swath of virtually intact dry forest, parts of which were selectively logged for *S. macrophylla* in 1989–2001 (Zimmerman *et al.* 2001). Forest in this region is evergreen with a deciduous component, and the climate here is strongly seasonal: 1600–2100 mm of rain per year is interrupted by a severe 3–4 month dry period (June–August) when virtually no rain falls (Grogan 2001).

STUDY SPECIES AND ITS SPECIALIST HERBIVORE

Swietenia macrophylla (King) (hereafter just *Swietenia*) is a large, long-lived, emergent tree capable of exceeding 35 m in height and 1.5 m in diameter (Lamb 1966). In the Pará region *Swietenia* is host to a putatively monophagous moth, *Steniscadia poliophaea* Hampson (Noctuidae: Sarothripinae) (Grogan *et al.* 2005; Norghauer *et al.* 2006a,b). Seeds are dispersed by wind during the dry season when adults shed their crown, and germinate best in the forest understorey (in October–November). These newly germinating seedlings are highly susceptible to attack by caterpillars, especially near parent trees (J.M. Norghauer, unpubl. data). Following plant establishment caterpillars appear to feed exclusively on young leaves of *Swietenia* seedlings and saplings up to 5 m tall, except that it is least active in *Swietenia* crowns (see Appendix B in Grogan 2001). Generation time from first instar to mature adult is roughly 18–22 days, which includes a 9–11 day cocooning period (J.M. Norghauer, unpubl. data). Unfortunately, little else is known about this caterpillar's biology, except that they are least active in the dry-season months for unknown reasons (Norghauer, unpubl. data; J. Grogan, pers. comm.). As elsewhere, vertebrates at Pinkaiti do not eat *Swietenia* seedlings (Lamb 1966). New leaves of both small and large *Swietenia* seedlings, regardless of light conditions, expand at a mean rate of 32% day⁻¹ (calculated following Kursar & Coley (2003); J.M. Norghauer, unpubl. data from a nursery experiment). Finally, natural densities of *Swietenia* seedlings are always highest near and, in this region, to the west of parents (within 30 m) because of prevailing dry winds. However, juveniles more than 50 cm tall are rarely found within 50 m downwind of reproductive trees (Grogan & Galvão 2006).

FIELD EXPERIMENT

We used a randomized block design to study the interactive effects of canopy cover and simulated leaf herbivory on seedling performance and subsequent attack by *S. poliophaea*. Seeds were collected during the previous dry season (July–August, 2002) near three fruiting *Swietenia*, mixed at camp, and then randomly sown individually in black polyvinyl sacs (12 × 20 cm, with perforated bottoms) filled with local soil. Seedlings were reared in a nursery enclosed by layered 30% shade-cloth that approximated understorey light conditions.

In early March 2003 we selected 14 light gaps situated = 50 m from the nearest reproductive *Swietenia* (defined as ≥ 30 cm d.b.h.) in an area of about 25 ha. These gaps were selected with their estimated proximity to conspecific adults in mind, and appeared to be

recently formed judging by the low vegetation growth (< 2 m tall, *sensu* Brokaw 1982). Nearest-neighbour distances between gaps averaged 120.4 m (± 55.2 SD, range = 70–280 m). Each gap was paired with an understorey location 30–45 m away from its edge on a random compass bearing; the two locations together formed an experimental block ($n = 14$). For the two gaps separated by only 70 m, bearings were aligned 180° to each other to place the two understorey locations as far apart from each other as possible. Hemispherical canopy photographs were taken at the centres of gap and understorey locations using a digital camera (Nikon Coolpix 850, Nikon, Japan) affixed with a 180° fisheye lens, and analysed using Gap-Light Analyser v.2.0 software (Frazer *et al.* 1999). Mean canopy openness in gaps was twice that in the understorey (respective means (± SE) were 14.1% ± 0.34 and 7.1% ± 0.14; paired *t*-test on log-transformed values: $t = 20.4$, d.f. = 13, $P < 0.0001$). Estimated yearly photon flux density transmitted was three times higher in gaps vs. understorey (respective means (± SE) were 12.8 mol m⁻² day⁻¹ ± 0.31 and 4.5 mol m⁻² day⁻¹ ± 0.16; paired *t*-test on log-transformed values: $t = 18.9$, d.f. = 13, $P < 0.0001$).

In mid March 2003, at each gap or understorey location, 12 *Swietenia* seedlings were planted (with intact soil cores) into pre-dug holes arranged into three groups of four seedlings each (24 seedlings per experimental block, total of 336 seedlings planted). Spacing between individuals within a group was 0.5 m, while spacing between the three groups was 2 m. All seedlings were healthy and relatively damage-free (< 2% leaf damage) and the surrounding gap vegetation was left intact. At planting, seedlings were *c.* 5 months old, and their average height and number of leaves and/or leaflets (± SD) were 22.4 cm ± 3.09 and 7.0 ± 1.69; $n = 336$, respectively. Using nursery seedlings instead of naturally established seedlings provided two advantages for testing our predictions: (i) it permitted control for size/age-related differences among plants, which may influence their compensatory abilities (Boege & Marquis 2005), and (ii) it permitted control for prior exposure to *S. poliophaea* caterpillars (Karban & Baldwin 1997).

Within each group, the four *Swietenia* seedlings we planted were randomly assigned to one of four defoliation levels (0%, 10%, 50% and 90% leaf area removed). These were applied 2 weeks post-planting by clipping the leaves across the midrib vein with a pair of scissors. We cut across the midrib because *S. poliophaea* also does so in cases of severe herbivory (> 50%). We chose this damage range because 304 natural *Swietenia* juveniles showed standing leaf area losses of 0–85% (average = 11.4%; Norghauer *et al.* 2006a). Unlike natural herbivory, which is highly variable among leaves and within compound leaves, we removed the same proportions of leaf tissue from all leaves present. Therefore, our experiment may have underestimated the true impact of folivory because plants may better compensate for a given amount of damage if evenly dispersed within the plant (Marquis 1992). Before clipping, the height (to growing tip, to the nearest mm) and root-collar diameter (to nearest 0.1 mm) of each seedling was measured and extant leaves were counted and marked with thin copper wire loosely wound on the petiole. New leaves across seasons were distinguished using both numbered wire ties and the leaf nodal positions on the stem. Total initial leaf area of each seedling (cm²) was estimated by summing leaf areas predicted from measured leaf widths ($y = 14.4x - 31.84$; $n = 121$ leaves, $R^2 = 0.925$).

During the next eight months, the seedlings were monitored for leaf production and damage caused by natural herbivores. The 8-month period included the late wet season (April–May), dry season (June–August), early wet season (September–October), and mid-wet season months (November–December 2003). Following Aide (1993), new

leaves that expanded and matured were quantified for both potential leaf area (to the nearest 0.25 cm²) as well as leaf area consumed by insects (to the nearest 0.01 cm²) using a transparent plastic grid. In the case of a missing leaflet(s), the potential area of the opposite leaflet, if present, or the average potential size of remaining leaflets, was used in calculations of total damage and potential leaf area (Aide 1993; Angulo-Sandoval & Aide 2000; Massey *et al.* 2005). All measurements were made by J.M.N. and 2999 new leaves and/or leaflets were measured over the 8 months. Natural herbivory, expressed as a mean percentage of leaf area damaged per season, was first averaged over each seedling, and then across each defoliation level per location. Specialist caterpillar attack and feeding was confirmed by periodic visits to locations during leaf expansion, and by tell-tale characteristic signs of residual damage on matured leaves (see Appendix B in Grogan 2001; Norghauer *et al.* 2006a). We confirmed the number of *Swietenia* adults (> 30 cm d.b.h.) within 125-m of each gap and understorey location, and measured their diameters at breast height (or above the buttress if present). At the experiment's end, in mid-December 2003, we tallied surviving seedlings and again measured their height and root-collar diameters.

STATISTICAL ANALYSES

The proportions of seedlings that survived the 8-month period was analysed using a REML estimation method in a nested mixed-ANOVA model (Proc Mixed, SAS vs. 8.2, SAS Inc., Cary, NC). Both canopy cover type (light gap vs. understorey) and simulated leaf damage (nested within canopy cover type) were designated as fixed effects, whereas block was a random effect. Similarly, nested mixed-ANOVAs were used to test the main and interactive effects of canopy cover and simulated herbivory on four performance-related variables: (i) height growth, (ii) basal stem diameter growth, (iii) leaf production, and (iv) average area of expanded leaves (cm²) including damage. These variables were expressed in relative terms: that is, growth was expressed as a proportion of initial seedling size. To satisfy model assumptions, the first variable was log-transformed and the second and third were square-root transformed, whereas the proportions of surviving seedlings were arcsine-square-root transformed. Experimental seedlings receiving the same defoliation treatment within the same location could not be considered independent units, so we averaged the three individuals in each defoliation treatment level to yield 112 replicates (i.e. 4 clipping levels × 2 canopy cover types × 14 blocks). Under the LRM prediction we expected the clipping level to be significant. For the PVH prediction, we expected not only a significant main effect of canopy cover on growth and amount of natural herbivory, but also a significant fixed effect of prior clipping on damage from specialist caterpillar. Under the hypothesis that these two factors would jointly influence JCM, we expected a significant effect of *Swietenia* adult density on seasonal levels of young leaf herbivory in light gaps.

We used multivariate analysis of covariance (MANCOVA) to evaluate natural leaf herbivory (square-root transformed) across the four measurement periods because the same *Swietenia* seedlings were measured repeatedly (see von Ende 2001 for details). This analysis was restricted to light gaps because understorey seedlings did not produce a leaf in each of the surveyed seasons, resulting in many missing cells that were not accommodated by MANCOVA. Following a significant MANCOVA result, the herbivory analysis was decomposed through a univariate analysis of covariance (ANCOVA, with Type III sum-of-squares) for each of the four seasons surveyed. The fixed effect was prior simulated leaf damage (0%, 10%, 50% and 90% removal). The number of conspecific adults (range: 0–4) within a 125-m radius of each gap was considered *Swietenia* density in the

MANCOVA and univariate ANCOVAs. We also used two additional variables to express *Swietenia* adult density within the 125-m radius of gaps: basal area of adults and the summed d.b.h. of the adults. The latter variable lends greater weight to the number of adults, rather than their individual sizes. Results were similar for all three variables used to measure *Swietenia* adult densities, so we present only the analysis using total adult d.b.h. because it provided the best model fit (Pillai's Trace F -values for the overall effect of *Swietenia* adult density was $F_{4,39} = 9.21$ for total d.b.h., compared to 8.13 and 8.89 for number of adults and basal area, respectively).

Results

LIMITING RESOURCE MODEL

Across the four levels of simulated leaf damage, mortality of *Swietenia* seedlings was 10 times greater in the understorey than in gaps (33% vs. 3%). In the understorey, 50% of seedlings with more than half their leaf area removed died whereas only 15% of non-defoliated individuals did, but no effects of leaf removal on seedling survival were detected in light gaps (Fig. 1, Table 1). Among gap seedlings with more than half their leaf area removed, only 5% died over the 8-month period.

Not surprisingly, canopy openness had a strong, positive effect on all aspects of seedling growth (main effect of light in models, Table 1, top). In gaps, however, 50% and 90% leaf removal (hereafter 'severe' removal) caused significant reductions in both relative height and root-collar diameter growth, whereas growth in the understorey was negligible irrespective of the amount of initial leaf area removed (Fig. 2a,c; see Table 1). Leaf production was not significantly affected by simulated herbivory. However, gap seedlings with 0% and 10% damage (hereafter 'low' removal) clearly produced more leaves that were, on average, significantly larger (with up to

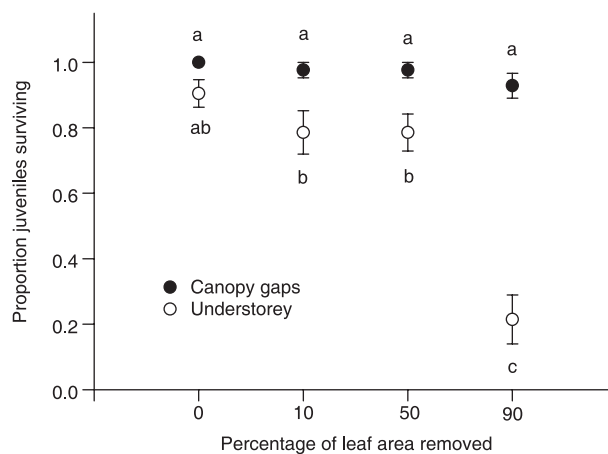


Fig. 1. Effects of simulated leaf herbivory on *Swietenia macrophylla* in two contrasting light environments on proportions of seedlings alive 8 months after planting. Means (\pm SE) are for 14 groups of three seedlings that received one of four leaf clipping removal treatments in the Pinkaiti forest, Pará, Brazil. Different lower case letters indicate significantly different least square means compared using a Tukey-Kramer adjusted posthoc test ($\alpha = 0.05$).

Table 1. Summary of statistical analyses used to test (i) the effects of light availability (shaded understorey vs. canopy gap) and leaf clipping (0%, 10%, 50% and 90% leaf area removal) on the performance of extant *Swietenia* seedlings at 14 blocks ($n = 112$, see Methods), and (ii) the effects of clipping and density of adult *Swietenia* trees (within a 125-m radius of gaps) on the seasonal variation in natural herbivory on *Swietenia* seedlings at the Pinkaití forest, Pará, Brazil ($n = 47$). The d.f. shown is the numerator in the models

		Survival		Height		Basal stem diameter		Leaf production		Average leaf size	
		F-value	P	F-value	P	F-value	P	F-value	P	F-value	P
Light	d.f.	76.6	< 0.0001	438.7	< 0.0001	321.7	< 0.0001	322.9	< 0.0001	35.9	< 0.0001
Clipping level (light)		18.2	< 0.0001	9.9	< 0.0001	11.3	< 0.0001	0.48	0.8230	5.88	< 0.0001
Model – 2LogLikelihood		60.3		49.4		113.2		121.5		97.8	
(2) MANOVA											
Total adult <i>Swietenia</i> d.b.h.											
Clipping level		F-value		P		Value		F-value		P	
d.f.	Value	F-value	P	d.f.	Value	F-value	P	d.f.	Value	F-value	P
12	0.439	1.76		4	0.485	9.21			< 0.0001		
Time (= season)											
d.f.	Value	F-value	P	d.f.	Value	F-value	P	d.f.	Value	F-value	P
3	0.613	21.17	< 0.0001	9	0.323	1.65		3	0.3	5.72	0.0024
Seasonal herbivory on <i>Swietenia</i> seedlings											
Late wet (April–May)		Dry (June–August)		Early wet (September–October)		Mid-wet (November–December)					
d.f.	F-value	P	F-value	P	F-value	P	F-value	P			
3	0.52	0.6732	1.55	0.2151	4.73	0.0062	0.50	0.6859			
1	0.00	0.9906	0.63	0.4319	38.2	< 0.0001	0.01	0.9308			
42											
<i>Follow-up univariate ANCOVAs:</i>											
d.f.	F-value	P	F-value	P	F-value	P	F-value	P			
3	0.52	0.6732	1.55	0.2151	4.73	0.0062	0.50	0.6859			
1	0.00	0.9906	0.63	0.4319	38.2	< 0.0001	0.01	0.9308			
42											

*The four dependent variables examined correspond to mean herbivory levels in each of four seasons over an 8-month period (April–December 2003, see Methods for details).

†Repeated measures analyses using traditional GLM for within-subjects effects yielded similar results.

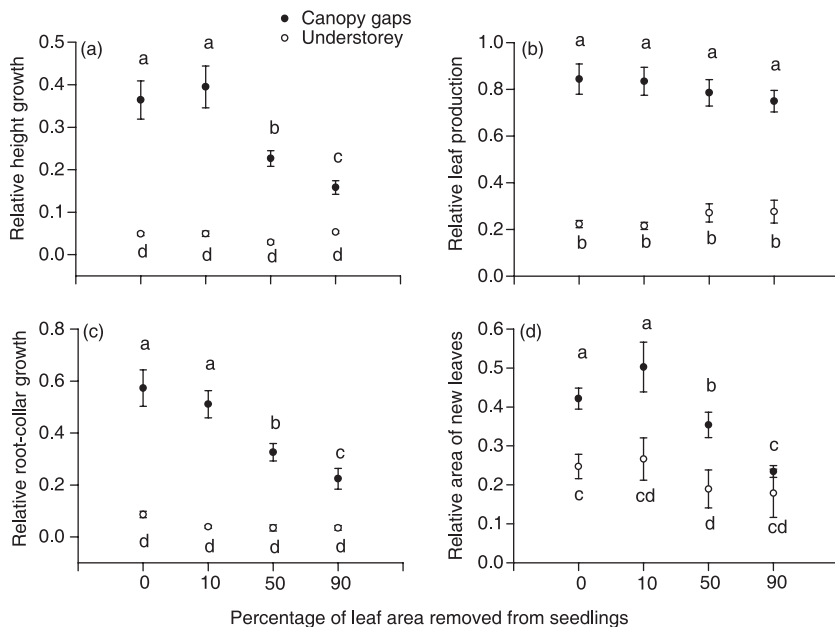


Fig. 2. Effects of simulated leaf herbivory on *Swietenia macrophylla* seedlings in two contrasting light environments on (a) relative height growth, (b) relative basal stem diameter growth, (c) relative leaf production, and (d) relative size of new leaves in surviving seedlings over the field experiment's 8-month duration. Means (\pm SE) are for 14 groups of three seedlings that received one of four leaf clipping removal treatments in the Pinkaití forest, Pará, Brazil. Different lower case letters indicate significantly different least square means compared using a Tukey–Kramer adjusted *post hoc* test ($\alpha = 0.05$).

eight leaflets) than seedlings with severe simulated leaf damage (Fig. 2b,d; Table 1).

Gaps were epicentres of greater food availability to potential herbivores of *Swietenia* young leaves. Over the 8 months, understorey seedlings produced far fewer leaves/leaflets (mean \pm SE, 2.2 ± 0.16 ; range 1.25–3.25) than gap individuals (15.7 ± 0.86 , range 9.7–19.6, Welch *t*-test: $t = 15.42$, adjusted d.f. = 13.86, $P < 0.001$; Fig. 3a). In fact, < 25% of understorey locations produced leaves in each of the four seasons, whereas all 14 gap locations consistently did throughout the 8-month period. Moreover, all understorey seedlings except one flushed a single leaf with the onset of rains, and most of these were small, simple leaves.

In absolute terms, individual height increments of gap seedlings with more intact leaf area (i.e. 0% and 10% removal) averaged approximately 9 cm over the 8-month period, reaching a maximum of 28.5 cm; whereas in the understorey increments were consistently low, averaging 1 cm (range = 0–3.1 cm). All *Swietenia* seedlings ended up with fewer leaves than they began with, but not necessarily with less total leaf area – a pattern also seen in juveniles of another shade-tolerant tree (*Shorea quadrivernsis*) with the same leaf area removed as here (Blundell & Peart 2001).

PLANT VIGOUR HYPOTHESIS

The vast majority of damage to new leaves that flushed after the clipping was caused by *S. poliophaea* caterpillars. Only two gap seedlings and one understorey seedling were grazed by another (unknown) caterpillar species, which fed gregariously from the leaf tip toward the petiole following leaf expansion. Leaf-cutting ants attacked recently expanded leaves of two additional gap seedlings. Otherwise all new leaves

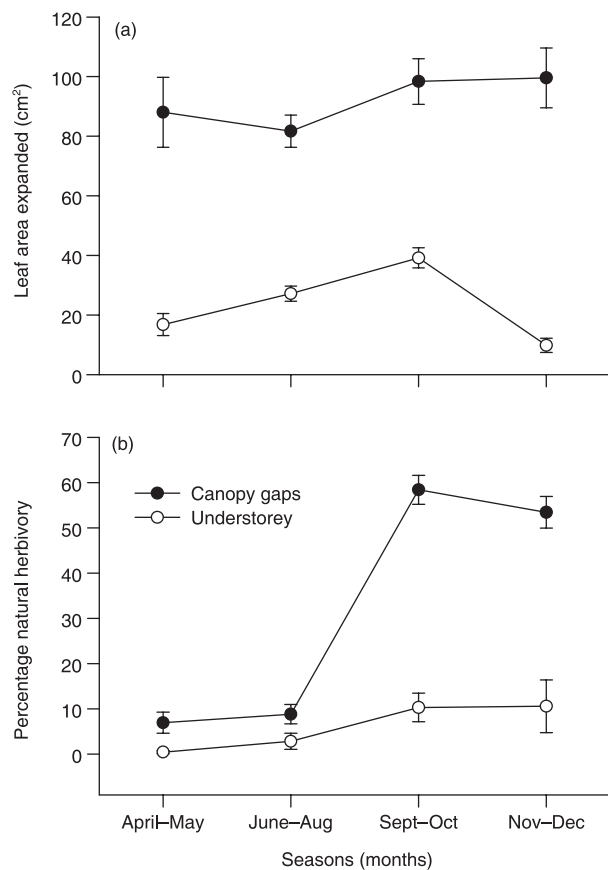


Fig. 3. Seasonal variation over the 8-month field experiment in the amount of (a) leaf area expanded of *Swietenia macrophylla* seedlings and (b) natural herbivory to new leaves (caused overwhelmingly by *Steniscadia poliophaea* caterpillars) growing in two contrasting light environments. Means (\pm SE) correspond to the 14 locations wherein all extant seedlings (1–3 per removal treatment) were pooled.

matured unscathed except those attacked by *S. poliophaea* caterpillars. No attacks by the Meliaceae shoot borer, *Hypsipyla grandella*, were observed. The results below include folivory from all insect agents, although > 99% of young leaves were damaged only by *S. poliophaea* caterpillars.

Herbivory was virtually absent in the late wet and dry seasons (medians: 0.15% and 0.70%, respectively), but exploded in the early wet season and remained high through the mid-wet season flushes (main effect of time (season) in Table 1; Fig. 3b). Every gap seedling produced 1–5 compound leaves in a synchronous single flush over a few weeks in each of the early and mid-wet season months. During this time, herbivory levels peaked and incidences of 100% defoliation were common. No apparent effects of leaf clipping on percentage damage to new leaves were detected in any of the seasons over the 8-month study period (MANCOVA repeated measures analyses: time \times simulated herbivory term, see Table 1).

JANZEN–CONNELL MECHANISM

We detected density-dependent herbivory in light gaps at the population level that was contingent upon the season in which *Swietenia* seedlings flushed their leaves (MANCOVA: significant time \times total adult d.b.h. interaction, see Table 1). Generally, we observed *S. poliophaea* activity within, and occasionally beyond, 125 m from the nearest reproductive *Swietenia*. However, in the early wet season, leaf area losses to *S. poliophaea* caterpillars in gaps increased significantly with the total d.b.h. of *Swietenia* adult trees (follow-up ANCOVA in Table 1, Fig. 4a). Also, within gaps, seedling variation in mean early wet season herbivory decreased with increased density of conspecific adults (Fig. 4c), suggesting that further away from adult(s) trees, some clipped seedlings suffered more damage than others (see above). These population-level, density-dependent effects in gaps disappeared for subsequent leaf flushes that occurred in the mid-wet season months (Fig. 4b,d), and were not detected in late wet and dry seasons

(all P -values > 0.4, Table 1). When we substituted distance (m) from gap to the nearest conspecific adult for total adult d.b.h. in the overall MANCOVA model, the result was not near significant ($P = 0.79$).

By contrast, in 10 out of 14 experimental blocks, new leaves of *Swietenia* seedlings in understory environments were undamaged by the specialist caterpillar. Seasonal attacks by *S. poliophaea* were not significantly affected by any measure of conspecific adult density (all P -values = 0.24–0.97). Four understory plots happened to be situated between 20 m and 50 m of an adult *Swietenia*, and the caterpillar attacks occurred exclusively on these seedlings; however, attacks varied substantially among seedlings within plots. Like the gap seedlings, this natural herbivory appeared unaffected by prior simulated leaf damage (mixed ANOVA, $-2LL = 161.6$, treatment term: $F_{3,32.6} = 1.05$, $P = 0.38$), so we pooled seedlings across clipping levels for further analyses. Average young leaf herbivory in near plots (< 50 m) exceeded plots beyond 50 m of an adult, in both the early wet season (Wilcoxon–Kruskal–Wallis test: $\chi^2 = 6.1$, $n = 13$, $P = 0.0136$) and mid-wet season months (Wilcoxon–Kruskal–Wallis test: $\chi^2 = 4.8$, $n = 9$, $P = 0.0281$; Table 2). These effects seemed absent during the late-wet ($P = 0.15$) and dry seasons ($P = 0.47$). Generally, understory herbivory in the early and mid-wet months was bimodal: *Swietenia* seedlings either suffered severe leaf area losses to *S. poliophaea*, or had negligible leaf damage.

Discussion

LIMITING RESOURCE MODEL

As predicted by the LRM, severe leaf area losses in the first growing season were lethal to *Swietenia* seedlings in the shaded forest understory, whereas in light gaps seedlings tolerated removal of up to 90% of their initial leaf area. Higher growth rates in gaps were not surprising given the higher insolation and strong selection pressure to reach the

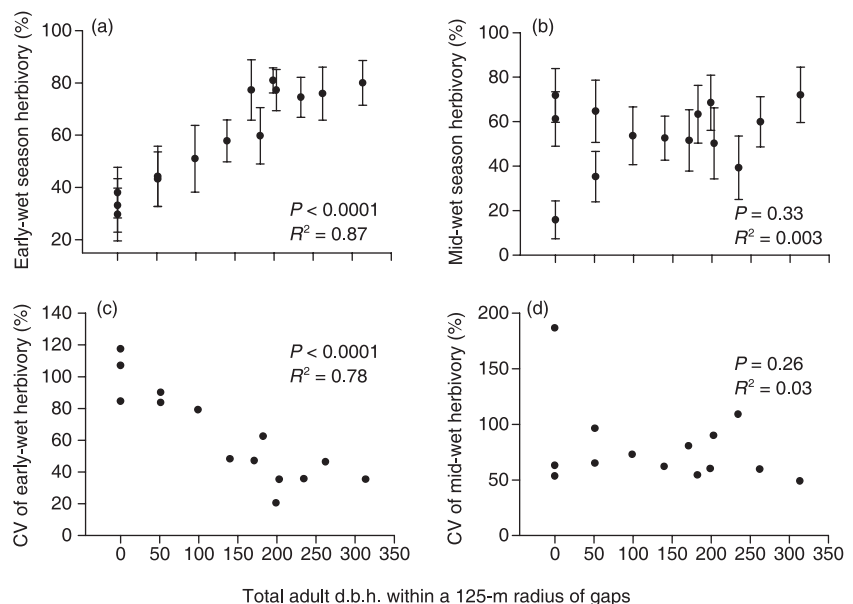


Fig. 4. Relationships between total d.b.h. of adult conspecifics within a 125-m radius of 14 canopy gap plots and mean (\pm SE) natural herbivory to new leaves of *Swietenia macrophylla* seedlings: (a) produced in the early wet season months (September–October 2003) and (b) produced in the mid-wet season months. The lower panel illustrates the coefficients of variation (CV) associated with the (c) levels of early wet season leaf damage and (d) levels of mid-wet season damage to all treatment seedlings in the 14 gaps at the Pinkaiti forest, Pará, Brazil. The R -squared values are adjusted for the sample size.

Table 2. Summary of post-clipping natural herbivory on young leaves in early wet and mid-wet seasons on extant understorey *S. macrophylla* seedlings at 13 block units (one block excluded where leaf-cutter ants caused severe defoliation). Plots were categorized as 'near' if they were < 50 m from nearest reproductive conspecific adult and 'far' if > 50 m

Distance	Early wet season (September–October)						Mid-wet season (November–December)					
	Mean (%)	SE	Median	Min–Max	CV	<i>n</i> *	Mean (%)	SE	Median	Min–Max	CV	<i>n</i> *
Near	20.5	6.8	22.7	0–100	66	4	26.0	13.9	26.9	0–100	107	4
Far	2.6	1.3	1.8	0–50.1	152	9	0.00	0.00	0.00	–	–	5

*Note: the *n* does not represent a single juvenile per se, but rather the number of understorey locations with survivor(s) used as replicates.

canopy in the competitive gap environment (Blundell & Peart 2001). Elsewhere in Pará, 78% of naturally established *Swietenia* seedlings in large, experimental canopy gaps (241–1006 m²) survived the first year, adding *c.* 25 cm in height, whereas in the shaded understorey only 33% survived and seedling growth was small (1 cm year⁻¹) (Grogan *et al.* 2005). Further, the fact that leaf production was not reduced under severe simulated herbivory (see Fig. 2b), even in the understorey, suggests that a seedlings' response to herbivory is prioritized towards maintaining an intact leaf area, regardless of canopy cover. In Borneo, Blundell & Peart (2001) reported the same interactive effects of canopy cover and simulated leaf herbivory on mortality of a shade-tolerant species (*Shorea quadrivermis*) in that 90% clipping reduced 8-month survival of juveniles in the understorey, but was tolerated in gaps. In Panama, variation in light levels across artificially created gap sizes did not affect the survival of *Trema micrantha*, a neotropical pioneer tree, despite differences in leaf damage between gap sizes (Pearson *et al.* 2003).

In the light-limited understorey, clipped *Swietenia* seedlings were unable to replace leaf area lost to simulated herbivory and appeared on a course towards death (see Fig. 2d). There, a single severe attack by *S. poliophaea*, or even repeated low-intensity attacks to the occasional new leaf, is apt to increase the risk of mortality to newly germinated seedlings, and is not helped by accumulating leaf fungal pathogens once seedling leaves have matured (Grogan *et al.* 2005; Grogan & Galvão 2006; J.M. Norghauer, unpubl. data). In a Costa Rican secondary forest, severe folivory during the first growing season was associated with higher mortality in *Swietenia* juveniles (Gerhardt 1998). We expect that escaping early leaf herbivory in the understorey is crucial for *Swietenia* seedlings to survive to the next growing season (Clark & Clark 1985; Grogan & Galvão 2006). However, it remains uncertain whether the compensatory advantage provided by gaps to *Swietenia* could be maintained indefinitely. Severe and chronic *S. poliophaea* attacks, coupled with shading from faster growing neighbours, can eventually kill seedlings in gaps, especially following canopy closure (Grogan 2001; J.M. Norghauer, unpubl. data).

PLANT VIGOUR HYPOTHESIS

One way to test the plant vigour hypothesis (PVH) is to experimentally generate fast- and slow-growing plants. We did that

in two ways: by placing *Swietenia* seedlings in high- and low-light environments and by cutting their leaves. In the latter case, however, it is not clear if clipping leaves may reduce attacks because of reduced vigour and/or induced plant responses that convey resistance, a problem that confounds such tests of PVH (Price 1991). In the present study this was a moot point because we found no significant support for PVH within gap or understorey locations wherein all clipped seedlings appeared equally susceptible to *S. poliophaea* caterpillars. This result is consistent with the idea that any induced plant defences are more effective against generalists than specialists, and presumably reflects coevolutionary history between *S. poliophaea* and *Swietenia macrophylla*, which may have allowed the caterpillar to overcome or cope with chemical defences (Thompson 1994; Karban & Baldwin 1997).

Irrespective of the clipping level applied, gap seedlings consistently suffered the most damage to new leaves in each of the seasons surveyed (see Fig. 3b). In contrast to the shaded understorey, light gaps function as reservoirs of primary productivity where young foliage is abundant and concentrated in space and time (Stanton 1983; Basset *et al.* 2001; Richards & Coley 2007). Leaf herbivory also was highest in thinned canopy treatments and on larger sized *Swietenia* juveniles attacked by an unidentified caterpillar in Costa Rica (Gerhardt 1998) and, elsewhere in Pará, by both *S. poliophaea* and the *H. grandella* shootborer (Grogan 2001; Grogan *et al.* 2005). Increased herbivore attacks of larger, vigorous seedlings and juveniles are known to occur in other tropical tree species as well (Gerhardt 1998; Prado & Vieira 1999; Sullivan 2003). For example, *Miconia argentea* seedlings grew faster in larger than in smaller-sized gaps, but also suffered more damage there when unprotected from herbivores, whereas *Trema micrantha* and *Cercopia insignis* showed opposite patterns (Pearson *et al.* 2003).

In a temperate rain forest in Chile, tree seedlings also suffered greater damage in gaps vs. understorey despite the former yielding higher foliar concentrations of phenols and condensed tannins that can function as antiherbivore defence compounds (Chacón & Armesto 2006). Although we did not test here for any increased allocation to such compounds in *Swietenia* seedlings in gaps vs. understorey – as predicted by the Carbon : Nutrient Balance hypothesis (CNBH) (Stamp 2003) – our results indicate that even if any such increases happened in young, expanding leaves, they did not deter herbivory from *S. poliophaea* caterpillars. We think that a more

explicit consideration of leaf age is paramount when testing LRM, PVH and CNBH to clarify the impact of herbivory on tree seedling dynamics. For example, problems may arise if recently expanded or mature leaves are used for bioassays of putative defence compounds when the bulk of damage happens quickly during the leaf expansion phase; or if whole leaf consumption and/or premature abscission (see Blundell & Peart 2000) are overlooked in measuring herbivore impacts.

JANZEN–CONNELL MECHANISM

Our study is novel for two reasons. First, it has revealed a pronounced increase in damage to the young leaves of seedlings by a specialized moth caterpillar as a function of the density of conspecific adults. Second, the spatial scale of density-dependent caterpillar attacks and damage was greater for tree seedlings growing in light gaps than in the shaded understorey.

SPECIALIST HERBIVORY AND REGULATION OF *SWIETENIA* POPULATIONS

Density-dependent herbivory may have important consequences for *Swietenia* population dynamics in this forest. Combined with the negative effects of simulated leaf damage on seedling growth and survival, and the specialist's clear bias towards attacks on larger, vigorous *Swietenia* seedlings under the conditions most favourable for recruitment (i.e. light gaps), our results indicate *S. poliophaea* caterpillars may generate a powerful Janzen–Connell effect on the *Swietenia* population. Sustained severe folivory ($\geq 50\%$) is likely to prolong the time *Swietenia* seedlings spend in smaller size classes, thus increasing their risk of mortality and slowing recruitment rates into the canopy in the vicinity of conspecific adults (*sensu* Sullivan 2003).

At the same time, it remains unclear whether the intense herbivory witnessed here would apply to single *Swietenia* juveniles established via long-distance dispersal events (≥ 75 m). *Steniscadia poliophaea* females may well have a harder time finding these lone individuals, especially amid heterospecific vegetation that could provide associational resistance (Root 1973; Grogan *et al.* 2005; Massey *et al.* 2005). Nevertheless, we have witnessed caterpillar attacks and signs of past attack on lone saplings in gaps at least 80 m downwind of the nearest *Swietenia* adult (which is what prompted the present study). Manipulative tests using varying conspecific seedling densities are needed to help resolve this question, and would be augmented by information on the fecundity of conspecific trees.

Three other studies have tested distance- and/or density-dependence with respect to insect herbivory on young leaves of trees. Barone (1996) found that for two of six tree species in Panama, herbivory to understorey saplings declined with distance from the nearest conspecific adult, but only in the early wet season (as found in the present study). Elsewhere, Blundell & Peart (1998) found that leaf damage to youngest leaves declined with increased distance from the nearest conspecific adult for understorey seedlings of two of four *Shorea* species

studied in a Bornean forest. In Puerto Rico, Angulo-Sandoval & Aide (2000) observed a positive relationship between leaf-miner herbivory to young leaves and sapling densities of *Manilkara bidentata*, which was unaffected by light availability, conspecific adult densities, or leaf phenology. The studies above, however, used natural seedlings/saplings and did not control for possibly differences in plant age; nor did they demonstrate detrimental effects of leaf area loss on plant survival and growth that are central to JCM. More recently, Sullivan (2003) demonstrated such negative effects of simulated stem-boring on *Tabebuia ochracea* saplings, and also observed scale-dependent shoot borer attacks at higher conspecific sapling densities within a 50-m radius (but not at 10-m) yet uncorrelated with distance to the nearest conspecific adult.

IS SPATIAL SCALE DIVERGENCE IN HERBIVORY DRIVEN BY LIGHT AVAILABILITY?

Many plot-based studies have since revealed that density-dependent tree mortality and recruitment is widespread in tropical forests (Harms *et al.* 2000; reviewed by Leigh 2004). Yet the functions and identities of biotic enemies responsible for these observed dynamics remain elusive (Sullivan 2003; Leigh 2004). Moreover, as Hubbell (2004) noted, '... we still do not know quantitatively and on what spatial scales the density dependence operates in each life history stage' (p. 18). This is a key consideration because if Janzen–Connell type effects remain highly localized (i.e. only near lone adult trees) it must weaken the extent to which herbivores can regulate tree populations over larger spatial scales in forests (also see Gunton & Kunin 2007).

Our results provide some insight on these issues. Density-dependent herbivory to *Swietenia* seedlings by a specialist moth caterpillar occurred on a much larger spatial scale (125 m) in gaps than in the surrounding understorey matrix. Moreover, while not the focus of this study, there also may occur fine-scale density dependence within 50 m of *Swietenia* trees (see Norghauer *et al.* 2006a). In other words, it was harder for *Swietenia* to escape the caterpillar in habitat most favourable for seedling growth – and especially when more conspecific adults were around. We illustrate this interaction between LRM, PVH and JCM in Fig. 5, and make two predictions about young-leaf chewing herbivores. First, with increasing light – and hence increasing plant tolerance and vigour – seedlings should, on average, become more attractive and apparent to herbivore(s). Second, the intersections show where sapling recruitment is maximized at low vs. high proximity to (or in low and high density areas of) conspecific adults.

The most plausible explanation underpinning this novel interaction, and our results in general, is that finding succulent *Swietenia* juveniles in light gaps will increase the average fitness of ovipositing *S. poliophaea* females relative to the understorey, a habitat where the caterpillar is essentially resource limited (Harrison 1987; Price 1991). To speculate, strong selection pressure may have shaped foraging behaviour of this moth to quickly locate young foliage by first searching

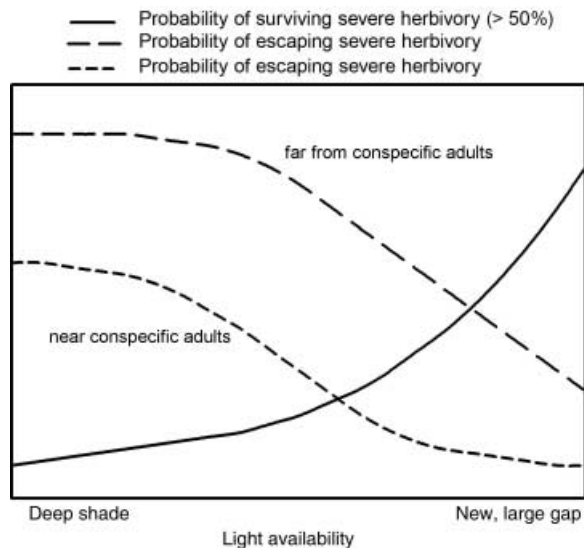


Fig. 5. Proposed modification of the Janzen–Connell mechanism that integrates effects of local light availability on the probability of tree seedling escape from herbivory to young leaves and tolerance to herbivory. The two dashed curves represent different proximities to conspecific adults: ‘near’ indicating seedlings with at least one adult within 50 m and multiple adults within a 125-m radius, and ‘far’ indicating no adults within 50 m and one or zero conspecific adults within a 125-m radius.

in the vicinity of *Swietenia* adults (Stanton 1983), and then by moving among high-light pockets in the forest (Bernays & Chapman 1994). Our results also favour the idea that specialist insect herbivores display extreme behavioural efficiency at locating hosts over long distances, likely aided by acute sensitivity to specific odours and/or visual cues of host and non-host plants alike (Bernays 2001). Tree ontogeny is an important caveat to keep in mind, however: that is, very young trees may acquire resistance to severe attacks once they reach a certain size: conversely, they may also face new herbivore threats (e.g. shoot borers; Stamp 2003; Boege & Marquis 2005). Lastly, our results agree with recent work in Panama by Richards & Coley (2007), who found greater lepidopteran densities on saplings in gaps vs. the understorey in a Panamanian forest and that ovipositing lepidopterans were able to respond quickly to leaf flushes in the early wet season. Caterpillars, especially moths, deserve more attention in studies of young tree dynamics in species-rich forests.

Conclusions

Our research suggests that LRM and PVH theory may yield a richer understanding of how the Janzen–Connell hypothesis may function in species-rich forests. Light gap driven increases in seedling tolerance to herbivory, coupled to higher food availability of young leaves in gaps, may force host-specific insect folivores to track this food resource and thus forage more widely in forests than previously thought. Therefore, a potential consequence is that seedling survival becomes dependent on the density of conspecific adult trees at a larger spatial scale, thus partly diminishing (but not

eliminating) the initial advantage of long-distance seed dispersal for escaping attacks from herbivores very near parent trees (Norghauer *et al.* 2006b; see Thomas 1990). In this way, the *Steniscadia poliophaea* moth herbivore may function to help limit the number of *Swietenia* adults in this Amazonian forest.

Acknowledgements

We are grateful to the Brazilian Government (CNPq and FUNAI) and the Kayapó community of A'ukre for permission to conduct research. Kaket, Kubanet and Biri-Biri Kayapó, and Nilson Vicente de Salles and Clarindo dos Santos Cruz helped incredibly in the forest. Logistical support at the study site was provided by Conservation International–Brazil. Discussions with A.A. Agrawal, P. Kotanen, T. Lambert, C. Nock, D. Peart, S. Smith and S.C. Thomas helped us prepare the manuscript, and an early draft was improved by comments from S.C. Thomas and J. Grogan, and a later version by F.P. Massey and two anonymous referees. This study was funded by the Donner Foundation Canada, the Natural Sciences and Engineering Research Council of Canada (J.R.M.), and a Doctoral Scholarship (J.M.N.) from Le Fonds Québécois de la Recherche sur la Nature et Technologies (Government of Québec, Canada).

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Received 21 May 2007; accepted 9 October 2007
 Handling Editor: Fergus Massey