

Juvenile mortality and attacks by a specialist herbivore increase with conspecific adult basal area of Amazonian *Swietenia macrophylla* (Meliaceae)

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Abstract: According to the Janzen–Connell model, host-specific natural enemies can promote species coexistence of canopy trees in tropical forests by attacking progeny where they are most concentrated. However, empirical evidence relating negative density-dependent mortality to herbivory and, in particular, attack by specialist herbivores, remains rare. We investigated density dependence in a natural population of *Swietenia macrophylla* in a south-eastern Amazon forest of Brazil. Across 24 adult trees, we found that initial juvenile densities were positively correlated with basal area of adult conspecifics whereas subsequent survivorship over 1 y for these juveniles declined strongly with increasing basal area of adult conspecifics. For 18 trees with > 5 juveniles surviving for 1 y, further evidence supporting the Janzen–Connell mechanism was obtained in that leaf herbivory and attack by a specialist microlepidopteran moth (*Steniscadia poliophaea*) increased, and overall foliar condition decreased, with conspecific basal area. Moreover, when differences in mean juvenile size (number of extant leaves) were accounted for, juvenile survival over 1 y decreased with increased specialist leaf herbivory. Collectively, these results indicate that herbivores, in particular *S. poliophaea*, may contribute to density dependence among *S. macrophylla* juveniles. We conclude that the survival of juveniles and their probability of recruitment into the canopy is decreased where conspecific adults are largest and/or most numerous and find support for the importance of host-specific pests in driving density dependence among tropical trees.

Key Words: bigleaf mahogany, density dependence, herbivory, Janzen–Connell model, seedlings, South-eastern Amazonia, specialist, *Steniscadia poliophaea*, *Swietenia macrophylla*, tropical forests

INTRODUCTION

Ecologists have proposed numerous mechanisms to explain the maintenance of the extraordinarily high species diversity found in tropical forests. In these species-rich communities, where myriad tree species share the same resources, population stabilizing mechanisms are thought to be essential for the maintenance of diversity (Chesson 2000). Demographic density dependence can stabilize populations through a causal link between changes in population sizes and demographic rates (Hixon *et al.* 2002). However, despite compelling evidence that density-dependent recruitment and mortality is pervasive in tropical forest communities (Harms *et al.* 2000, Peters 2003, Webb & Peart 1999, Wills *et al.* 1997), the biological mechanisms responsible for generating these

dynamics remain poorly understood (Hyatt *et al.* 2003, Leigh 2004, Sullivan 2003, Wright 2002).

Janzen (1970) and Connell (1971) independently proposed a negative density-dependent spacing mechanism that would promote tree species coexistence in tropical forests (Chesson 2000). In what has since been dubbed the Janzen–Connell model of tropical tree diversity (Clark & Clark 1984), adult recruitment is hypothesized to be low where natural enemies attack and kill densely packed progeny near conspecific adults, which liberates space and resources for recruitment by other species. As emphasized by Connell (1971), for this spacing mechanism to be effective, these enemies must have specialized diets, a key assumption in the model (Barone 1998).

Although the Janzen–Connell model was proposed more than three decades ago, important gaps remain in subsequent tests of the model's mechanisms in natural forests. Significant among these is a failure to identify specific agents causing density-dependent mortality

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(Hubbell 2004, Leigh 2004). Of particular interest are insect herbivores (Coley & Barone 1996), which because of their high fecundity and short life cycles, are able to respond numerically to rapid increases in resource availabilities of their host plants. In their review, Hammond & Brown (1998) concluded that invertebrates caused stronger density- and/or distant-dependent mortality of seeds than vertebrates. A similar conclusion may apply at the seedling stage; however, to date, most studies of the Janzen–Connell mechanism have focused on the seed stage. In most tests of the mechanism that have examined invertebrate herbivory at the juvenile stage, the specific agents were not identified (Blundell & Peart 1998, Clark & Clark 1985, Mack *et al.* 1999, but see Sullivan 2003).

A second research gap is that virtually all studies in natural forests have focused on distant and/or density dependence in the vicinity of isolated individual trees (Hammond & Brown 1998, but see Schupp 1992). Little attention has been devoted to concentrations of conspecific adults despite the fact that the Janzen–Connell model does not preclude adult aggregations (Becker *et al.* 1985, Blundell 1999, Clark & Clark 1984) and that many tropical tree species show some degree of spatial clumping (Condit *et al.* 2000, Hubbell 1979). Indeed, such adult aggregations may intensify the mechanisms driving density-dependent processes (Janzen 1970). It is also possible that responses of natural enemies at single trees may not be indicative of their responses in adult aggregations; for example, enemy satiation may occur at sufficiently high adult densities (Schupp 1992). Seedling density dependence can only promote species coexistence if it continues to operate where conspecific adults share overlapping seed shadows (all else being equal) (Webb & Peart 1999). Density-dependent herbivory across a full range of adult tree sizes and densities, from isolated trees to adult aggregations, remains unexplored.

Here, we examine patterns of juvenile mortality of *Swietenia macrophylla* King (Meliaceae). This species is of particular interest in a Janzen–Connell context because seedlings are attacked by the specialist moth, *Steniscadia poliophaea* Hampson (Noctuidae: Sarrthropinae). Larval instars of the species feed exclusively on expanding tissue of *S. macrophylla*, but appear to be absent from both adult crowns and from saplings greater than 5 m in height and from other tree species (Grogan 2001, Norghauer, unpubl. data). Attacks by the Meliaceae shoot-borer, *Hypsipyla grandella*, a well-known pest in many plantations, do not appear to be common in natural or secondary forests (Grogan *et al.* 2005). *Swietenia macrophylla* also is of interest because although it is the most commercially valuable neotropical timber species and was recently listed on CITES Appendix II, its regeneration ecology in natural forests has been rarely investigated and remains contentious (Brown *et al.* 2003,

Grogan *et al.* 2003, 2005). Because natural enemies may respond most vigorously at aggregates of adults where overlapping seed shadows potentially concentrate progeny, we studied both isolated and aggregated adults in a natural population of *Swietenia macrophylla*. Specific objectives of the research were to determine whether: (1) survival of *S. macrophylla* juveniles decreased with increasing conspecific adult basal area; (2) standing levels of juvenile foliar damage increased, and foliar condition decreased, with increasing conspecific adult basal area; and (3) attacks and damage by the specialist invertebrate herbivore, *S. poliophaea*, on juveniles increased with conspecific adult basal area. To our knowledge, this is the first study to examine relationships between juvenile mortality and attack by a specialist folivore that includes both isolated and clumped adults.

METHODS

Study site and species

The study was conducted at the Kayapó Centre for Ecological Studies (Pinkaití) located in the Kayapó Indigenous Area (KIA), Pará, Brazil (7°46'14"S, 51°57'43"W). The Centre occurs within a *c.* 8000-ha reserve that, unlike the surrounding areas of the KIA, has never been logged for mahogany (Zimmerman *et al.* 2001) and retains a natural population of *Swietenia macrophylla* mapped within a core area of *c.* 600 ha (Grogan 2001). Although the majority of adult *Swietenia macrophylla* in the reserve are widely scattered and relatively isolated from one another, they are sometimes found in clumps of 2–6 per ha. Approximately one-third (37%) of mapped adult trees (>30 cm dbh) have at least one conspecific (>10 cm dbh) within a 55-m radius. Mean annual rainfall is approximately 1700 mm, with a severe 3–4-mo-long dry season in June–September (<50 mm of rain, Lambert *et al.* 2005, Zimmerman *et al.* 2001).

In the 600-ha area of *Swietenia macrophylla* concentration, 24 *S. macrophylla* trees (49–169 cm dbh) were selected for study. Eighteen adults were isolated in that they were >70 m from the nearest conspecific adult (≥ 30 cm dbh). The six remaining adults occurred in concentrations: four had another nearby adult (within 56.5 m radius) and two had four nearby adults (within 56.5 m radius). Nearest neighbour distances between the 24 trees averaged 226 m (range: 72–550 m).

We reasoned that natural enemies should respond more vigorously not only to larger than smaller adults, but also at aggregations of adults where overlapping seed shadows potentially concentrate seedling progeny. Hence, we used conspecific adult basal area per ha (hereafter adult BA) as a proxy for seedling densities. This served three important functions. First, adult BA is

positively correlated with seed production in *Swietenia macrophylla* (Grogan & Galvão in press, Gullison *et al.* 1996, Pinto 2003). Secondly, adult BA measured at a larger spatial scale can reflect not only changes in tree size, but also tree density. Thirdly, using adult BA bypasses the problem of non-independence that arises when relating seedling survival to seedling densities (Brett 2004, Jackson & Somers 1991, Webb & Peart 1999). Therefore, in addition to measuring the basal area of each individual, we also measured the total basal area of adults in the surrounding 1-ha area (i.e. within a circle of radius 56.5 m). All selected adults had fruited at least once within the previous 2 y (i.e. 2001 and 2002).

In April 2004, for a subset of 15 trees, per cent canopy openness at 5, 15 and 30 m from each tree was measured using a handheld spherical densiometer (Lemmon 1957) along two transects (N and W of the tree). At each distance on the transects, densiometer measurements were the average of four measurements made facing N, W, S and E.

Juvenile survivorship, herbivory and foliar condition

In April 2003 (late wet season), all *Swietenia macrophylla* juveniles within a 30-m radius of each adult tree (2826 m²) were counted and marked with a wire stake flag. Approximately 50% of all seeds land within 30 m of the parent, and up to 75% within 50 m, mostly to the west of parent crowns (Grogan & Galvão in press, Norghauer, unpubl. data). In the case of paired adult trees, we placed the 30-m-radius circle around the most westerly of the two adults. For the two higher concentrations, we selected the most centrally positioned tree. The majority of juveniles were < 30 cm in height (maximum height 46 cm). To better focus on the coming mortality period, the few juveniles that displayed signs of early drought, leaf wilting or poor rooting were ignored. One y later, again in April, we determined which individuals had survived, and for adults with at least five survivors ($n = 18$), as detailed below, we measured standing levels of overall herbivory and foliar condition.

For each surviving juvenile, the number of leaf nodes and extant leaves was recorded. Also, for each extant leaf, herbivory was quantified as the total percentage of missing photosynthetic leaf area, which was estimated visually to the nearest 5%, with 1% assigned to leaves with $\leq 1\%$ herbivory. All herbivory measurements were made by one observer (J. M. Norghauer). A linear regression comparing visual estimates of per cent damage to actual damage of the same leaves measured with a transparent plastic grid (Aide 1993) showed that the rapid visual estimation technique was very effective ($R^2 = 0.97$, $n = 50$ leaves, $P < 0.0001$). Herbivory included damage caused by insects, including *S. poliophaea* (see below), and by leaf fungal pathogens (Garcia-Guzman & Dirzo 2001),

as well as areas colonized by epiphylls (Coley & Kursar 1996). We found no evidence of herbivory by vertebrates. Although necrotic areas could result from either grazing by insects or fungal activities, necrotic damage was minor (less than 1% of leaves surveyed).

Following Blundell & Peart (1998), we also employed mean per cent tissue retention over all nodes as a measure of foliar condition. Such measurements are important because young expanding leaves of mahogany juveniles attacked by *S. poliophaea* caterpillars are highly susceptible to premature abscission (Norghauer, unpubl. data), hence missing leaves on juveniles may indicate cryptic herbivore effects (Blundell & Peart 2000). This calculation assumes that under herbivore-free conditions, all leaves produced by a plant would be retained. This is a reasonable assumption given that unless juvenile *Swietenia macrophylla* leaves suffer significant damage they can survive for more than 1 y (Norghauer, unpubl. data).

Finally, for each surviving juvenile, we measured: (1) the proportion of leaf area damaged by *S. poliophaea* compared with all other sources and (2) incidence of *S. poliophaea* attack. Flushing leaves that escaped 100% defoliation or premature abscission display characteristic signs of herbivory by *S. poliophaea* (Appendix B in Grogan 2001). Direct observations during caterpillar feeding (Norghauer, unpubl. data) confirmed these signs (Figure 1), namely: (1) one or more midrib lesions and scarring visible on leaf underside (at least one near the petiole), (2) characteristic irregular chewing along the leaf edges, (3) numerous tiny holes (< 2 mm diameter) on expanding leaves, which can remain through leaf maturation if eggs were laid late in the leaf's expansion (Aide & Londono 1989), and (4) fine webbing and frass. We are yet to observe any other insect feeding on expanding leaves of *Swietenia macrophylla*. Once expanded, however, other signs of insect activity are occasionally found, but the damage is markedly different, likely owing to the different defence features of mature leaves (e.g. leaf toughness). Nonetheless, we took a conservative approach in our assessments in the field: any doubtful signs of specialist attack were not scored. The proportion of damage due to *S. poliophaea* compared with all other sources was calculated on a per leaf basis and subsequently averaged across leaves for each juvenile and then across juveniles for each adult. The proportion of surviving juveniles with at least one leaf that showed one or more of the above indicators of attack was used as a measure of incidence of specialist attack.

Data analysis

We used weighted linear regression to analyse 1-y survivorship of *Swietenia macrophylla* juveniles as a

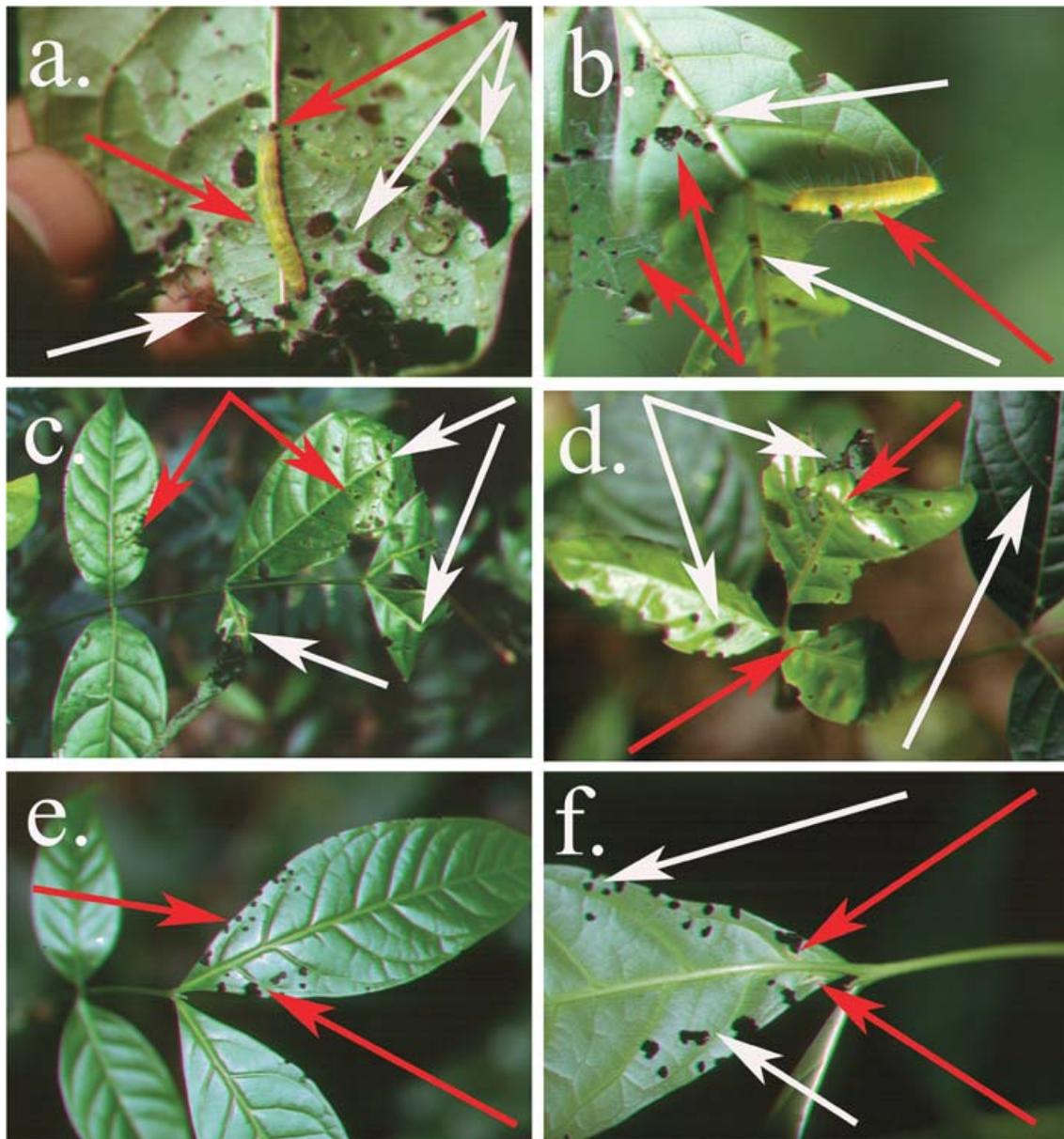


Figure 1. Characteristic types of damage caused by caterpillars of *Steniscadia poliophaea* to young leaves of *Swietenia macrophylla* juveniles in the south-eastern Amazon. (a) A final-instar caterpillar (approximately 2 cm long, red arrow) feeding on the underside of a juvenile leaf; note the distinctive midrib lesion visible (long red arrow) and other parts of the leaf that display characteristic holes and irregular leaf margins (white arrows); (b) Leaflet underside showing a late-instar caterpillar (red arrow), and several midrib lesions (white arrows) and frass and webbing (pair of red arrows) associated with larval feeding and development; (c) View of a typical compound leaf attacked during its expansion showing residual damage (red arrows); note collapsed leaflets caused by midrib lesions (white arrows) often associated with severe leaf area loss; (d) A young expanding compound leaf with the distinctive collapsing of damaged leaflets associated with midrib lesions (red arrows), irregular shaped holes (> 2 mm), and chewing at the edges; in the background, a previously undamaged leaf that is now mature and characterized by intact, dark green leaflets (single white arrow); (e) Surface view of a compound leaf discovered late in its expansion by ovipositing female moths with negligible overall damage from caterpillars in the form of characteristic numerous small holes (< 2 mm) and irregular chewing along leaf edges (white arrows); and (f) Underside view of the compound leaf show in (e) with two early-instar caterpillars (red arrows) responsible for the characteristic damage. All photos were taken by J. M. Norghauer at the Pinkaití forest reserve, Pará, Brazil.

function of adult BA, with initial number of juveniles as the weighting factor. This analysis corrects for the fact that the precision of a given survival estimate is expected to vary as a function of the original numbers of seedlings.

For adults with at least five juvenile survivors ($n = 18$), we also used weighted linear regressions to examine mean number of leaves per juvenile, average per cent damage of extant leaves, foliar condition and the incidence of

specialist attack as a function of adult BA. Mean foliar condition, mean number of leaves and mean per cent damage attributed to the specialist were log-transformed to meet assumptions of normality and homoscedasticity.

We also tested whether any observed effect of adult BA on survival could be attributed to either specialist attacks or light levels by examining whether the adult BA effect remained once either the incidence of specialist attack ($n = 18$) or light levels ($n = 15$) were first entered in the model. Adult trees were the unit of replication in all analyses. For the family of regressions, beginning with $\alpha = 0.05$, we applied the sequential Bonferroni correction to reduce the chance of making a Type I error (Rice 1989).

Finally, we tested whether the implicit assumption of spatially independent errors among focal trees was a reasonable one by contrasting the fit of the independent errors model against one in which the error term was assumed to have an explicit spatial structure (as estimated from the semivariogram of the residuals). Specifically, a likelihood ratio tested the hypothesis that the spatial parameter (ρ) equalled zero by computing the log likelihood difference between the independent errors and spatial covariance models (Littell *et al.* 1996). In our case, the independent errors models were deemed sufficient for all dependent variables investigated ($0.0 < \chi^2 < 2.2$, $df = 1$, $P > 0.05$). All analyses were conducted using SAS (v. 8.02.).

RESULTS

Initial abundances of *Swietenia macrophylla* juveniles measured in April 2003 within circles of 30-m radius around the 24 adult trees increased markedly with adult basal area within a 56.5-m radius ($r^2 = 0.50$, $n = 24$, $P < 0.0001$; Figure 2a). Juvenile densities ranged from 5 per 0.28 ha^{-1} at a single isolated adult (dbh = 78.1 cm, adult BA = $0.48 \text{ m}^2 \text{ ha}^{-1}$) to a peak of 142 per 0.28 ha^{-1} centred around two large, heavy-fruiting adults 11 m apart (dbh = 113.4 and 131.5 cm, adult BA in the circle with radius 56.5 m = $2.37 \text{ m}^2 \text{ ha}^{-1}$). However, the proportion of juveniles surviving to the following year declined dramatically as a function of adult BA (adult BA log-transformed, $r^2 = 0.47$, $n = 24$, $P = 0.0002$; Figure 2b). The highest proportion of juveniles surviving (0.72) was observed around an isolated parent that had last fruited in 2001 (Norghauer, unpubl. data) and the lowest (0.13) at an adult with four nearby conspecifics. Considering only isolated adults (and thus excluding adult BA values $> 2.24 \text{ m}^2 \text{ ha}^{-1}$), a disproportionate number of juveniles died near larger-sized parents ($R^2 = 0.55$, $n = 18$, $P = 0.0012$).

On a per juvenile basis, per cent leaf damage ranged substantially (0–85%). There was no evidence of meristem damage by *Hypsipyla grandella*. On a focal-tree

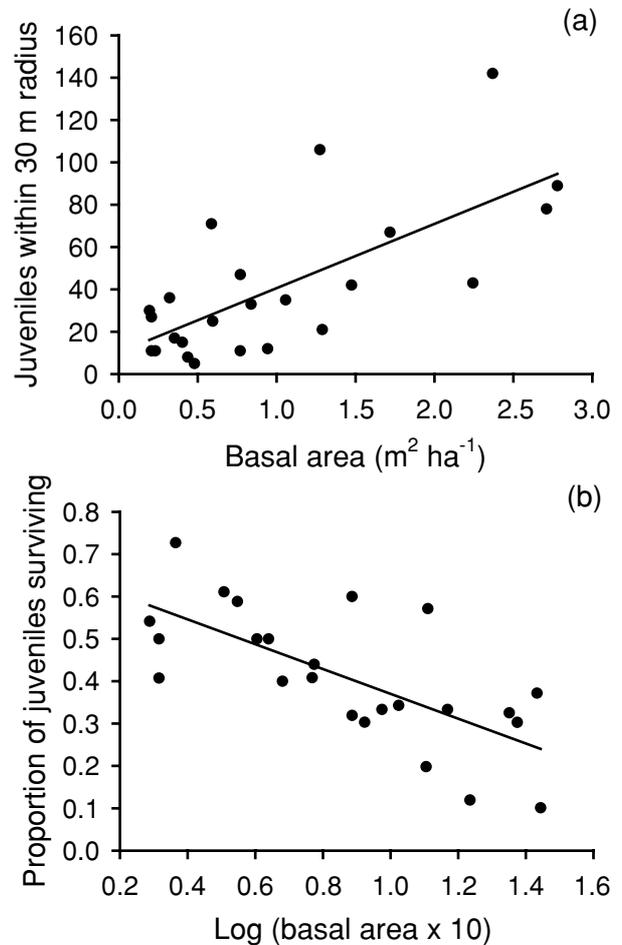


Figure 2. Relationship between conspecific adult basal area within a 56.5-m radius at 24 *Swietenia macrophylla* in the south-eastern Amazon and (a) number of naturally established *Swietenia macrophylla* juveniles within a 30-m radius and (b) proportion of *Swietenia macrophylla* juveniles surviving 1 y later. Regression lines are $y = 30.4x + 10.3$ and $y = -0.284x + 0.630$, respectively.

basis, mean per cent herbivory on surviving juveniles increased significantly with adult BA ($R^2 = 0.55$, $n = 18$, $P = 0.0005$; Figure 3a) and foliar condition declined strongly with adult BA ($R^2 = 0.52$, $n = 18$, $P = 0.0008$; Figure 3b). Both the incidence of attack by caterpillars of the specialist herbivore, *S. poliophaea* ($R^2 = 0.75$, $n = 18$, $P < 0.0001$; Figure 4a), and the per cent leaf area they damaged increased dramatically with adult BA ($R^2 = 0.68$, $n = 18$, $P < 0.0001$; Figure 4b). Further, of the eight focal adult areas that had no signs of specialist attack, six were isolated. When the incidence of specialist attack was partialled out, the effect of adult BA on juvenile survivorship became non-significant (Type III linear partial regression $F_{1,17} = 4.48$, $n = 18$, $P = 0.0514$), indicating that adult BA was a much weaker predictor when its association with specialist attack was taken into account. In contrast, when mean per cent

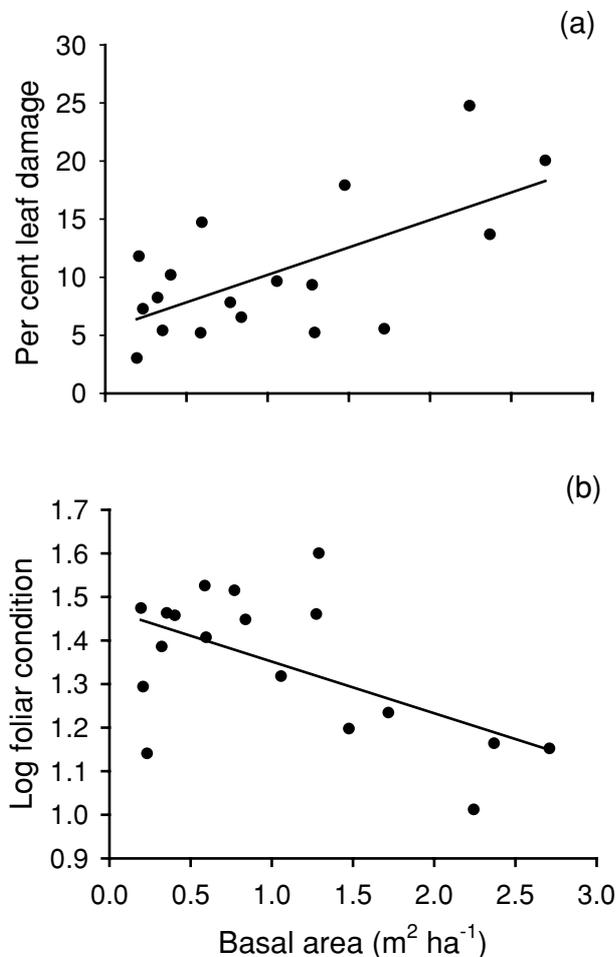


Figure 3. Relationship between conspecific adult basal area within a 56.5-m radius at 18 *Swietenia macrophylla* trees in the south-eastern Amazon and (a) mean per cent leaf herbivory of surviving *Swietenia macrophylla* juveniles and (b) mean foliar condition of surviving *Swietenia macrophylla* juveniles. Regression lines are $y = 5.02x + 4.85$ and $y = -0.138x + 1.50$, respectively.

damage solely from non-specialist agents (i.e. fungi and other insects) was partialled out, adult BA remained a highly significant predictor of juvenile survivorship (Type III linear partial regression $F_{1,17} = 11.6$, $n = 18$, $P = 0.0039$), suggesting that herbivory due to agents other than *S. poliophaea* was not the main factor resulting in the negative relationship between adult BA and survivorship. Further, when proportions of leaf area damaged by *S. poliophaea* were excluded, overall herbivory levels (log-transformed) did not significantly increase with adult BA ($R^2 = 0.10$, $n = 18$, $P = 0.192$). Finally, although we did not experimentally assess whether *S. poliophaea* drove observed mortality patterns, when the mean number of leaves (log-transformed) was held constant, the probability of 1-y juvenile survival decreased as both per cent damage (log-transformed) and incidence of attack by the *S. poliophaea* increased (Type III linear partial

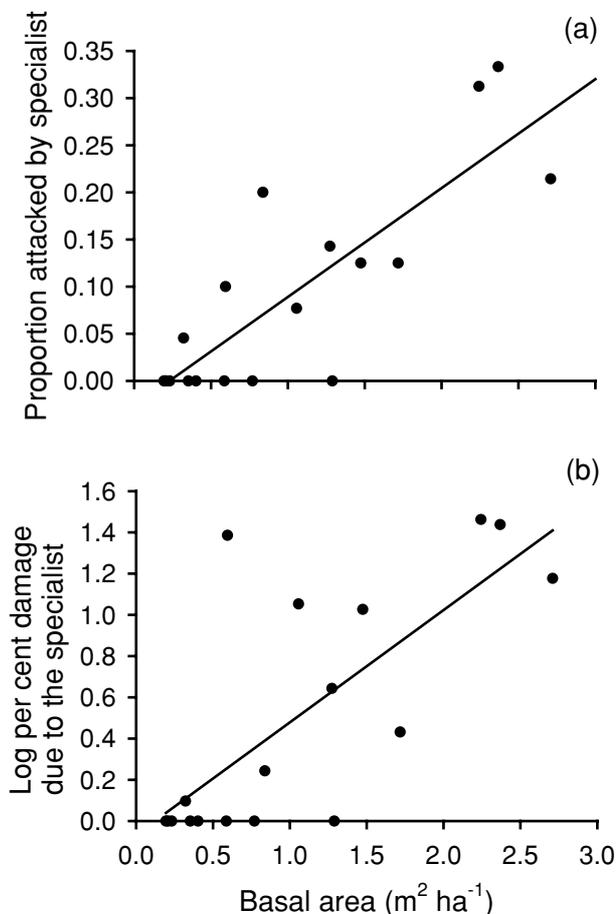


Figure 4. Relationship between conspecific adult basal area within a 56.5-m radius at 18 *Swietenia macrophylla* trees in the south-eastern Amazon and (a) the proportion of surviving mahogany juveniles attacked by caterpillars of the specialist herbivore, *Steniscadia poliophaea*, and (b) mean per cent leaf herbivory attributed to caterpillars of *Steniscadia poliophaea*. Regression lines are $y = 0.123x - 0.0312$ and $y = 0.574x - 0.0918$, respectively.

regressions, respectively, $F_{1,17} = 2.5$, $n = 18$, $P = 0.0415$ and $F_{1,17} = 7.3$, $n = 18$, $P = 0.0017$). Although the number of leaflets and/or leaves observed on surviving juveniles ranged substantially (1–40), mean plant size at the tree level was not significantly correlated with 1-y survival ($R^2 = 0.01$, $n = 18$, $P = 0.645$).

In addition to greater herbivory, juveniles in areas of higher adult BA also had fewer extant leaves on average (log-transformed) ($R^2 = 0.40$, $n = 18$, $P = 0.0048$) and had a lower proportion of nodes with retained leaves ($R^2 = 0.41$, $n = 18$, $P = 0.0043$), despite the fact these same areas were associated with greater canopy openness and, presumably, greater understorey light availability ($R^2 = 0.47$, $n = 15$, $P = 0.0051$). Not surprisingly given the light-loving nature of *Swietenia macrophylla*, canopy openness was a significant predictor of lifetime leaf production in surviving juveniles: over 50% of the variation in the mean number of nodes was explained

by increasing canopy openness ($R^2 = 0.52$, $n = 15$, $P = 0.0025$) and mean number of nodes was positively correlated with adult BA ($R^2 = 0.39$, $n = 18$, $P = 0.0059$). Yet despite the fact that canopy openness and leaf production were positively associated with adult BA, survivorship still strongly declined. When canopy openness was included in the model, juvenile survival still decreased with adult BA (log-transformed) (Type III partial linear regression, $F_{1,17} = 7.17$, $n = 15$, $P = 0.021$).

DISCUSSION

Focal adults and juvenile densities

The initial juvenile counts suggest that the recruitment of *Swietenia macrophylla* juveniles is seed limited in that greater local seed inputs at higher adult BA gave rise to larger juvenile populations (Makana & Thomas 2004, Svenning & Wright 2005). Our data do not preclude possible negative density-dependent processes acting prior to establishment; however, they do suggest that negative density dependence in the juvenile stage may act to partially reverse these differences due to local fecundity. In a Bornean forest, Blundell & Peart (2004) also found evidence of recruitment limitation and a similarly striking reversal of density dependence in juvenile abundance for *Shorea quadrinervis* (Dipterocarpaceae), especially among relatively large juveniles.

Juvenile dynamics, herbivory and foliar condition

In addition to survivorship, we pursued four ancillary lines of evidence in examining the role of herbivory in influencing population dynamics of juveniles: overall per cent leaf damage and foliar condition, and incidences of attack and per cent leaf damage caused by a known specialized enemy (caterpillars of *S. poliophaea*). In areas of increasing adult BA, a greater proportion of juveniles died and surviving juveniles had more leaf damage, fewer leaves, lower proportions of leaves retained, lower overall foliar condition and higher incidences of specialist attack as well as higher levels of specialist damage. Taken together, these results are consistent with Janzen–Connell mechanism and implicate herbivory by leaf pathogens and invertebrates, in particular *S. poliophaea*, as a key biological mechanism driving negative density dependence in *Swietenia macrophylla* at the study site. Most convincingly, the adult BA effect was significant when damage by *S. poliophaea* alone was examined (Figure 4b), but not when leaf area damaged by *S. poliophaea* was excluded. At the same time, these results are correlational and additional manipulative tests are required to definitively establish the role of *S. poliophaea*

in causing *Swietenia macrophylla* mortality; for example, use of exclosures or pesticides to exclude insect herbivores from juveniles planted out across levels of adult sizes and densities.

Mechanisms other than herbivory by natural enemies could lead to decreased survival of *Swietenia macrophylla* at higher adult BA and seedling densities. Intraspecific competition is an unlikely scenario here because of the low densities of juveniles that we observed, which at most averaged 0.05 juveniles m^{-2} (142 marked juveniles at a pair of large adults). In addition, strong negative effects of competition might be expected to have an impact on leaf production (Coomes & Grubb 1998); instead, in areas of increasing conspecific adult BA, where annual mortality was greatest, *Swietenia macrophylla* juveniles had produced more leaf nodes. Damping-off pathogens (Augspurger 1984) unlikely contributed to density dependent mortality here because we marked juveniles in April, when they were already well established. Increased shading from *Swietenia macrophylla* adults also is not a mortality factor here because we found a positive relationship between adult BA and canopy openness. Increased litterfall also seems unlikely, because in other fieldwork litter depth was not significantly correlated with either adult BA or with juvenile survival (Norghauer *et al.*, unpubl. data). Lastly, mortality induced by dry-season moisture stress in *Swietenia macrophylla* (Grogan 2001) may have been exacerbated in the deeply shaded understorey where juvenile root systems are less well developed (Fisher *et al.* 1991, Gerhardt & Fredriksson 1995). In this regard, moisture stress may have been expected to weaken any adult BA effect by increasing mortality in areas of low adult BA where canopies were more closed.

Specialist herbivory and density-dependent regulation of tropical trees

Our quantification of both attack and damage specific to *S. poliophaea* suggest that it is the candidate most likely responsible for the density-dependent mortality of mahogany juveniles. This conclusion agrees with Grogan (2001), who noted that ‘over the course of their life times few seedlings escaped *S. poliophaea* attack’, and ‘*S. poliophaea* was the principal cause of mortality at the four trees with highest initial seedling densities’ (p. 219). The significance of *S. poliophaea* for the population dynamics of *Swietenia macrophylla* is supported by subsequent work at our study site, where we found strong negative effects of simulated herbivory (leaf clipping) on juvenile growth, survival and leaf retention, and decreased vertical growth, leaf production and leaf area of planted juveniles attacked by *S. poliophaea* caterpillars (Norghauer, unpubl. data). Similarly, in a seasonal forest

in Costa Rica, Sullivan (2003) reported significantly higher mortality in *Tabebuia ochracea* (Bignoniaceae) as sapling and shoot densities increased due to a specialist shoot-boring moth.

Furthermore, because juvenile mortality increased with increasing parent size among isolated trees, it appears that *S. poliophaea* responds directly to increasing seedling densities, or to greater frequency of fruiting events associated with tree age, or a combination of both. Similarly, Schupp (1988) found a negative relationship between tree size and survival of seeds under a subcanopy tree, *Faramia occidentalis* (Rubiaceae). Although we found that mortality weakened the positive relationship between *Swietenia macrophylla* juvenile numbers and adult BA ($R^2 = 0.20$, $n = 24$, $P = 0.0266$), it was insufficient – at least within 1 y – to completely reverse the increase in juvenile densities with adult BA. Intense specialist attack where adult BA was higher, however, may reduce juvenile growth rates and eventually lead to lower net recruitment. Unfortunately, very little is known about the role of highly specialized herbivores in regulating populations of tropical trees (Coley & Barone 1996), and aside from the observations of Grogan (2001) and our own, little is known about *S. poliophaea*.

Studies documenting negative density-dependent recruitment and mortality consistent with the Janzen–Connell mechanism have implicated invertebrate herbivores and pathogens (Harms *et al.* 2000, Leigh 2004, Peters 2003, Webb & Peart 1999, Wills *et al.* 1997). However, the actual processes driving these patterns remain unknown because few studies have yet quantified levels of damage to seedlings or saplings or identified the specific mortality agents (Coley & Barone 1996). Blundell & Peart (2004) suggested that insect herbivores are driving the density-dependent population dynamics of a dominant rain-forest tree, *Shorea quadrinervis*. However, their low-density treatment had an average of approximately 6 adults ha^{-1} – which corresponds to the high densities of mahoganies at our site – and the difference in levels of herbivory to juveniles between high and low adult densities were modest at best (respectively, 3.3% and 1.8%, from Blundell 1999). Recently, Ahumada *et al.* (2004) found that rarer tree species in a Panamanian forest (BCI) displayed stronger negative density-dependent juvenile dynamics. An unexplored possibility is that the observed rarity of many canopy trees species reflects consistently strong pressure by specialized herbivores.

CONCLUSIONS

In conclusion, the patterns of mortality and herbivory reported here lend support to the Janzen–Connell mechanism and for the first time implicate the importance

of attacks by a known specialist herbivore on juveniles at both the scale of single adults and across varying adult densities. Greater knowledge of natural history and more field research are needed to identify and experimentally ascertain the role of insect herbivores, particularly specialists, in order to evaluate and predict their contribution to driving negative density dependence in trees and the maintenance of diversity in tropical forests. Such research may be especially fruitful for relatively rare tree species.

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