PLANT ANIMAL INTERACTIONS

Julian M. Norghauer · Jay R. Malcolm
Barbara L. Zimmerman · Jeanine M. Felfili

An experimental test of density- and distant-dependent recruitment of mahogany (*Swietenia macrophylla*) in southeastern Amazonia

Abstract According to the Janzen–Connell model, high mortality of seeds and seedlings in proximity to conspecific adults can help maintain species diversity in tropical forests. Using a natural population of big-leaf mahogany (*Swietenia macrophylla* King), we tested the model's mechanism by examining seed predation and juvenile recruitment in the forest understory and in treefall gaps in the vicinity of both isolated and clumped adults. We used tethered seeds placed in three types of exclosure plots: (1) complete access to seeds, (2) semi-access (access by small-sized seed predators) and (3) no access (all mammals excluded). Exclosure treatments were applied within the understory (both near and far from adults) and in gaps at eight fruiting adults in the late dry season (2001) and scored ten months later. Significantly more seeds were removed in canopy gaps near clumped adults than at isolated adults; otherwise, none of the treatment factors significantly influenced seed predation. In contrast, understory juvenile recruitment was significantly enhanced by distance from adults and was twice as high at isolated than clumped adults, providing novel support for the Janzen–Connell mechanism. No-access exclosures protected significantly more seeds than semi- and full-access exclosures, implicating small mammals in seed losses. Across the eight trees, juvenile recruitment in the no-access exclosures decreased significantly with conspecific adult densities, implicating non-mammalian density-responsive factor(s) in mortality following germination; likely a known specialist invertebrate herbivore. When all treatments were combined, conspecific adult basal area and total DBH explained 72 and 90% of variation in overall juvenile recruitment, respectively. Collectively, these results indicate that Janzen–Connell effects can operate in *S. macrophylla*, especially during the seed-to-seedling transition, and will likely reduce recruitment in areas of high conspecific densities. They also suggest that further research into the causes of density-dependence in tropical trees should investigate mortality agents following germination.

Keywords Canopy gaps · Herbivory · Janzen–Connell model · Seed predation · Seedlings

J. M. Norghauer (✉) · J. R. Malcolm
Faculty of Forestry, University of Toronto,
Earth Sciences Building, 33 Willcocks Street,
Toronto, ON, Canada M5S 3B3,
E-mail: jules.norghauer@utoronto.ca
Tel.: +1-416-4846911
Fax: +1-416-9783834
E-mail: jay.malcolm@utoronto.ca

B. L. Zimmerman
Brazil Program, Conservation International,
1919 M St. NW, Washington, DC, 20036, USA
E-mail: bzimmerman@conservation.org

J. M. Felfili
Departamento de Engenharia Florestal,
Universidade de Brasília 70 919 970,
CP 04357, Brasília, DF, Brazil
E-mail: felfili@unb.br

Introduction

The vast number of coexisting trees species in tropical forests has long perplexed ecologists. One mechanism that promotes this diversity is density-dependent mortality, which can promote species coexistence by stabilizing population sizes through reductions in population growth rates (Chesson 2000). Seeds and seedlings represent the most vulnerable stage in a tree's development (Harper 1977) and density-dependent processes are thought to occur most strongly during these early post-dispersal stages when individuals are most abundant and susceptible to mortality (Howe and Smallwood 1982; Hammond and Brown 1998). Knowledge of the biotic and abiotic factors that influence density-dependent mortality during these early stages may be critical for better understanding and prediction of the structure and dynamics of tree populations and communities. Post-dispersal seed and seedling agents of mortality include vertebrates, invertebrates, and pathogens, all of which

can significantly alter patterns of seedling recruitment and reproductive success, and hence have the potential to exercise profound ecological and evolutionary forces on tropical tree populations and communities.

Almost 35 years ago, Janzen (1970) and Connell (1971) independently proposed that distant- and/or density-responsive natural enemies could drive the mutual repulsion of conspecifics and lead to disproportionate mortality of progeny near parent trees. This high mortality might in turn liberate areas for colonization and recruitment by other tree species and thereby contribute to maintenance of high local diversity. Two general predictions follow from their original conceptual model. First, rates of mortality should decrease with distance from a parent. Secondly, where seed shadows of two or more reproductive adults overlap, mortality driven by natural enemies should be greater than around single adults (all else being equal).

The numerous tests of the Janzen–Connell mechanism have yielded mixed support for the first prediction (reviewed in Clark and Clark 1984; Hammond and Brown 1998; Hyatt et al. 2003). A recent generalization, which supports one of Janzen's (1970) original suggestions, is that the survival advantage gained by distant dispersal appears to be more prevalent when the major predators are invertebrates rather than vertebrates (Hammond and Brown 1998; Wright 2002). As yet, the second prediction remains largely untested. To date, most studies have focused almost exclusively on isolated focal trees. Schupp (1992) pointed out more than ten years ago that studies at the population level are sorely needed; however, they remain rare with respect to biological processes driving mortality during the seed-to-seedling transition phase. An important but largely unexplored issue is the extent to which the response of natural enemies to host seed and seedlings around isolated trees are predictive of their response across varying conspecific adult densities. Will responses intensify, remain similar, or be reversed (for example, owing to enemy satiation, sensu Janzen 1971)?

A second weakness of research to date is that most post-dispersal studies have focused on mortality in the seed stage and have ignored subsequent juvenile recruitment. Studies that simultaneously address seed losses and seedling recruitment across multiple adult densities are rare. This is unfortunate given that many species offer fertile ground for such tests in that they have distributions characterized by both clumped and isolated adults (Condit et al. 2000). Such studies also may be required for a full test of the model's mechanisms; for example, even if negative density-dependent mortality is absent during the seed stage, it may emerge during the seed-to-seedling transition or juvenile stage (Terborgh et al. 1993).

Another important research gap is our knowledge about the role of canopy cover. As noted by Hammond and Brown (1998), canopy disturbance in the form of treefalls and crownfalls, although recognized as a predominant feature of tropical forests, has yet to be explicitly incorporated into field tests of the Janzen–Connell mechanism (e.g. Augspurger 1984; Schupp 1988; Cintra and Horna 1997). Both the frequency and size of canopy gaps can presumably alter the response of natural enemies and/or the susceptibility of their hosts to mortality. Canopy gaps, albeit unpredictable in space and time, may represent areas for colonization and enhanced recruitment (sensu Howe and Smallwood 1982) and may buffer the detrimental effects of natural enemies (Hammond and Brown 1998), especially among seedlings (Augspurger 1984; Wenny 2000). Seed-seedling conflicts may also occur in some species (Schupp 1995), as have been suggested for example for big-leaf mahogany (Grogan 2001). Seed survival may be reduced in gaps relative to the understory, but survival and growth of juveniles may be enhanced due to increased light levels. The influence of canopy gaps on density- and distant-dependent attacks by natural enemies and on mortality remains largely uninvestigated.

In this paper, we report on experimental field studies conducted on a canopy emergent tree, *Swietenia macrophylla* King (Meliaceae), an endangered species renowned for its high timber value, but one whose regeneration ecology remains controversial (Snook 1996; Brown et al. 2003; Grogan et al. 2003b). We employed a factorial combination of different types of exclosures and tethered seeds placed at low and high adult densities in an undisturbed population of mahogany to ask:

1. Is seed predation and juvenile recruitment density- and/or distant-dependent across varying adult densities?
2. How are patterns of seed predation and juvenile recruitment influenced by canopy cover?
3. Are small mammals important predators of mahogany seeds?

To our knowledge, this is the first field study to experimentally test the underlying mechanism of the Janzen–Connell model in the context of both varying adult densities and local light environments.

Materials and methods

Study site

The study was conducted at the Kayapó Centre for Ecological Studies (Pinkaití), a biological research station and forest reserve located in the Kayapó Indigenous Area (KIA) in the state of Pará, Brazil (7°46′14″S; 51°57′43″W). The Centre occurs within a ca. 8,000-ha reserve of lowland tropical, semi-deciduous forest in a region that annually receives between 1,600 and 2,100 mm of rain, with a severe three- to four-month dry season in June–September that receives < 50 mm of rain (Grogan 2001; Zimmerman et al. 2001; Lambert et al. 2005). Although most of the KIA has undergone extensive selective logging, the Pinkaití reserve has never been logged (Zimmerman et al. 2001) and retains a

natural population of mahogany with all size classes represented (up to 180 cm DBH) mapped in a core area of ca. 600 ha (Grogan 2001). The majority of adult mahoganies are relatively isolated from one another (>70 m apart), but they are also found in clumps of 2–6 per ha. The impact of subsistence hunting by the Kayapó on the vertebrate community appears to be negligible in the Pinkaití reserve (Lambert et al. 2005).

Study species

Big-leaf mahogany is a large and long-lived, fast-growing deciduous canopy emergent tree capable of exceeding 1.5 m in diameter and 50 m in height (Lamb 1966). Generally, fruiting is rare in individuals < 30 cm DBH and there is a positive relationship between tree size, consistency of annual fruit events and number of fruits produced per season (Gullison 1996; Grogan 2001; Snook et al. 2005). During the dry season (June–August), fruit capsules dehisce and the winged diaspores are dispersed by prevailing south-easterly trade winds, generating a predictable seed shadow: approximately 50% of diaspores fall within 30 m of the parent (and up to 75% within 50 m), mostly to the west of the parent crowns (Grogan and Galvão 2006; J.M. Norghauer, unpublished data). These diaspores consist of a seed (1.3–2.6 cm long by 0.8–1.3 cm wide, Grogan 2001) encased in a copper-coloured spongy endocarp that is relatively large, measuring 5–13 cm in length and weighing 0.19–0.96 g (mean = 0.56 ± 0.11 g SD, $n = 3,090$ diaspores; J.M. Norghauer, unpublished data). Mahogany seed germination (October–November) is triggered by moisture accumulation during the early rainy season and seeds germinate more rapidly in the shaded forest understory than canopy gaps (J.M. Norghauer et al., in preparation; Morris et al. 2000; Grogan and Galvão 2006). Disperse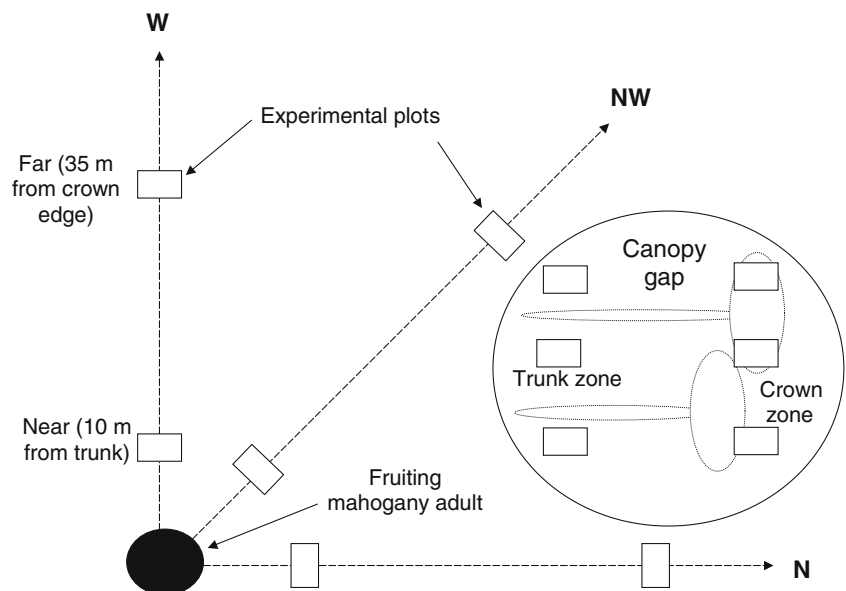d seeds are susceptible to predation by rodents. The meristematic stems and leaves of seedlings are highly susceptible to attack by caterpillars of a mahogany specialist moth, *Steniscadia poliophaea* Hampson (Noctuidae: Sarrothripinae) (Grogan 2001).

Experimental design

We designed an experiment to investigate seed predation by vertebrates in two contrasting light microhabitats (forest understory and canopy gap) and across varying adult densities: relatively isolated (low-density) and clumped (high-density) adults. In late July 2001, we selected eight fruiting trees (52–160 cm DBH) that occurred within an area of 200 ha (minimum convex polygon). Nearest neighbour distance between the eight trees ranged from 388 to 1,400 m, and the mean ($\pm$ SD) was 625 ± 325 m. The mean ($\pm$ SD) distance between them, based on a Euclidean minimum spanning tree, was 694 ± 333 m. Four of these were isolated at least 100 m from other adults (i.e., trees ≥30 cm in DBH); the remaining four had one to four adults within 50 m. In addition to their density, trees were selected based on the presence of a recently formed treefall gap of at least 350 m^2 in an area that was located downwind within < 70 m of the tree and where vegetation was < 2 m tall. In clumped areas we selected the most westerly fruiting tree. The distance from the selected tree to the gap edge was similar (*t*-test, $df = 6$, $P = 0.61$) between the low- and high-density trees [respective means ($\pm$ SD) were 42.8 ± 31.8 m and 33 ± 16.2 m]. In the context of Turner's (2001) review of the JC mechanism, our sample size of eight trees was above average. For the 28 trees species that he listed, the mean sample size of adults was 5.9 (range = 1–28), with a median value of 4 (see his Table 4.10).

Around each tree we established 12 replicate plots (1.0×1.5 m), six in each of the two microhabitats (see Fig. 1). Along bearings of W, NW, and N, one plot was

Fig. 1 Schematic representation of the experimental design showing the plot locations and the four treatments arrayed within the two light microhabitats downwind of mahogany adults. The two dispersal distances, which were nested within the forest understory microhabitat, were "near" and "far". The two gap zones, which were nested within the gap microhabitat, were "trunk" and "crown" (*circular inset*). See text for details

placed in the shaded understory 10 m from the adult trunk ("near") and one in shaded understory 35 m from the adult's crown edge ("far"). The remaining six plots were placed in the canopy gap: three in each of the "trunk" and "crown" zones of the gap and spaced 4–5 m apart along a transect that bisected each zone. Each plot contained 15 tethered seeds anchored to five wire flags (three per flag) arrayed in a pattern that approximated a density of seven seeds per m^2, which is within the range of natural seed densities observed near fruiting adults (J.M. Norghauer, unpublished data). Where the seed hull joined the wing, each seed was glued using epoxy to a 45-cm-long piece of fishing line. The three seeds per flag were spaced equally apart around it. The glue was tested for resistance to water and it was found that seeds remained attached despite periodic watering simulating early rains. The advantage of tethering seeds is that although some natural movement in the litter is accommodated, it also guarantees their location and provides for a more accurate assessment of seed fates over time (Schupp 1988). We are unaware of any experimental artefacts introduced by tethering seeds, but presume that any such effects were similar in magnitude across all plots. Large, freshly fallen mahogany diaspores (mean = 0.74 ± 0.073 g SD, $n = 1,440$) were collected for the experiment from under two heavily fruiting adults in July 2001. We used only undamaged, winged diaspores that were carefully checked for viability by gently pressing on the seed hull containing the embryo and by looking for holes made by boring insects and signs of pathogens.

In both microhabitats, we used three exclosure treatments, one per plot: (1) no exclosure (complete access), (2) a small mesh (1.5 by 2.5 cm mesh) chicken wire exclosure that excluded the abundant terrestrial rodents at the site (*Oryzomys* spp. and *Proechimys* spp.; see Lambert et al. 2005) (no access), and (3) a large mesh chicken wire exclosure (4.0 by 7.5 cm mesh) that permitted entry by small mammals that eat seeds (semi-access). Exclosures housed one seed and were cylindrical in shape (20 cm diameter by 40 cm high) and closed at the top in a pyramid-like fashion to prevent the collection of falling litter and debris. Exclosures were secured at their base with spikes so that the mesh was tight against the ground. Complete access, no-access, and semi-access exclosure treatments were randomly applied to the three plots in each level of the nested factors (i.e. near and far for understory and trunk and crown for gap). All experimental seeds and exclosure treatments were established in the late-dry season (August 16–30th, 2001), when natural seed dispersal was nearly completed. Within plots, individual exclosures that were toppled and/or flattened, presumably by large mammals, were not included in the analyses.

For each of the eight trees, in the surrounding ha (i.e., a circle of radius 56.5 m) we determined the DBHs and basal areas of adult mahoganies (≥30 cm DBH), including the focal tree itself. We used two related independent variables to express the abundance of mahoganies in the ha: total basal area of adults and the summed DBHs of the adults (both measured per ha). The latter lends greater weight to the number of adults, rather than their size. Basal area of mahogany in the clumped areas averaged more than twice that in the isolated areas [respective means ($\pm$ SE) were 1.81 ± 0.45 m^2 ha^{-1}, $n = 4$, and 0.86 ± 0.47 m^2 ha^{-1}, $n = 4$]. Similarly, summed DBH was greater in the clumped than the isolated areas [respective means ($\pm$ SE) were 225.25 ± 19.9 cm and 102.95 ± 25.9 cm)].

Seed predation and juvenile recruitment

We inspected the experimental plots ten months after they were established; namely, at the onset of the dry season in June 2002. Mahogany seeds were predated by rodents in a characteristic fashion and sometimes had discernible toothmarks on the winged seed remnants (see also Grogan 2001). The individually tethered seeds were visually categorized [as slightly modified from Terborgh et al. (1993)]: (1) live seedling present, (2) seed germinated with dead seedling remains, (3) entire seed missing, (4) seed embryo missing, but hull and endocarp present with or without rodent teeth marks, (5) seed endocarp intact, but with signs of insect predation, (6) seed endocarp intact, but soft to touch and dead, and (7) seed intact and viable. From these data, we calculated two measurements of seed fates: the proportion of seeds predated by vertebrates per plot (sum of categories 3 and 4; hereafter "vertebrate predation") and the proportion of seeds alive as juveniles (category 1; hereafter "juvenile recruitment"). In estimating vertebrate predation, we equated seed removal with predation; specifically, we assumed that seeds found missing were either immediately eaten at tethered locations or some time later if they were cached by rodents (Jansen et al. 2002).

Data analyses

For each of the two dependent variables we used a balanced, partly nested analysis of variance to maximize statistical power (see p. 301–338, Quinn and Keough 2002). Following those authors, adult density was the fixed, between-plot factor; the eight adult trees served as replicates for low ($n = 4$) and high adult density ($n = 4$) and also as a random blocking factor in the model. Microhabitat and exclosure type were the fixed, within-plot factors that used seed plots within the blocks as their scale of replication. Distances of "near" and "far" were levels nested within the understory treatment, and "trunk" and "crown" zones were levels nested within the canopy gap treatment. Importantly, again following Quinn and Keough (2002), we specified the appropriate error terms in the F-ratio denominators that tested the main and interactive effects of these fixed factors. Interaction terms that received little statistical support ($P > 0.15$) were removed from the model to increase statistical power. In the event of a significant main effect,

a post hoc comparison of means was performed by the Ryan–Einot–Gabriel–Welsch (REGW) multiple range test, as recommended by Quinn and Keough (2002). For significant interaction(s) terms we employed a Tukey–Kramer adjusted multiple comparison of the least-squares (LS) means test based on the final ANOVA model. Both dependent variables were arcsine square root transformed to meet assumptions of normality and homogeneity. All statistical analyses were carried out using PROC GLM in SAS (v. 8.02).

Results

Seed predation

We found little evidence of distant-dependent vertebrate predation of *S. macrophylla* seeds. Seeds sown in the understory near and far from adults appeared to be equally susceptible to predation (ANOVA, $F_{(2,95)} = 1.492$, $P = 0.2322$). In addition, the intensity of seed predation was similar between the gap and shaded understory microhabitats (ANOVA, $F_{(1,95)} = 0.31$, $P = 0.581$). However, there was a significant interaction between adult density and microhabitat (ANOVA, $F_{(1,95)} = 5.81$, $P = 0.018$). Seeds placed in canopy gaps near clumped adults suffered nearly 50% more vertebrate predation than seeds in canopy gaps near isolated adults (Fig. 2; Tukey–Kramer pairwise test, $P = 0.0084$), but seed removal in the shaded understory was similar between low and high adult densities (Tukey–Kramer test, $P > 0.05$).

The exclosure treatments had by far the strongest effect on vertebrate predation of mahogany seeds (ANOVA, $F_{(2,95)} = 91.3$, $P < 0.0001$). Exclosures excluding all vertebrate predators had the lowest level of seed predation and had significantly less predation than exclosures accessible only to small-sized mammals (Fig. 3).
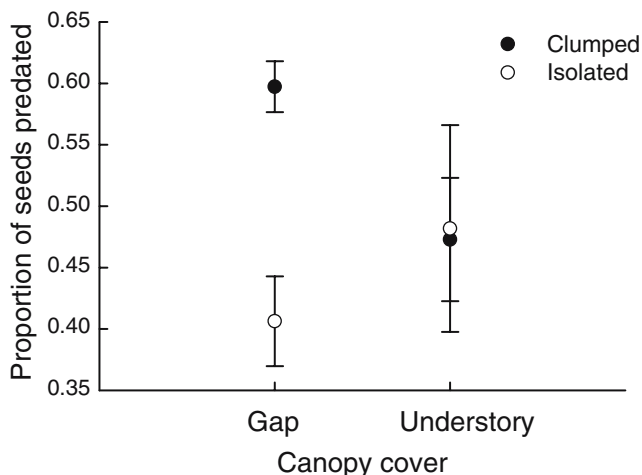
Fig. 2 The proportion of mahogany seeds scored as being predated by vertebrates (see text for details) in canopy gaps and the forest understory at low and high densities of adult mahoganies. Values are means ± 1 SE
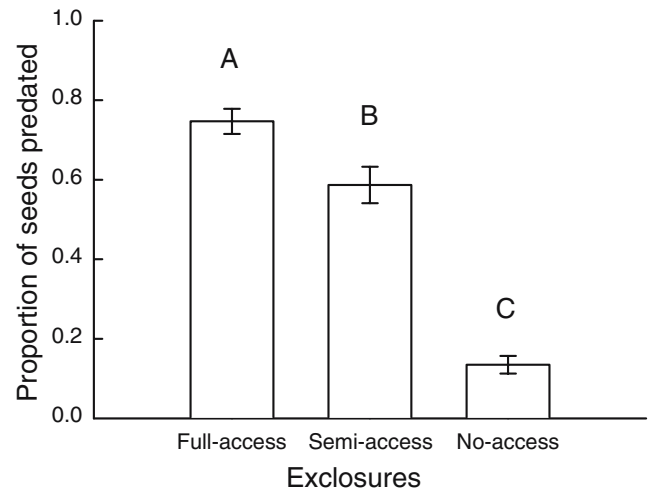
Fig. 3 The effect of the type of vertebrate exclosure on the proportion of seeds predated. Different letters indicate significant differences at $P = 0.05$ among means using REGW multiple comparison test. Values are means ± 1 SE

Predation levels in the full-access plots were nearly five times greater than in the full exclusion treatment, but approximately equivalent to those in semi-access plots (Fig. 3), suggesting that small mammals were the primary agents of seed removal.

The effect of the exclosure treatments also varied significantly with adult density (ANOVA, $F_{(2,95)} = 3.70$, $P = 0.029$). At isolated adults, complete access and semi-access exclosures had similar vertebrate predation rates (Tukey–Kramer pairwise test, $P = 0.551$), whereas at clumped adults, slightly more seeds were removed from complete access than the semi-access plots (Tukey–Kramer, $P = 0.051$). Comparing full-access plots only, more seeds were predated near clumped than isolated adults (83 vs. 66%, respectively; Tukey-Kramer test $P = 0.046$), regardless of the light environment.

Across all study plots, approximately 7.5% of experimental seeds displayed some signs of insect activity. No viable seeds were encountered ten months after sowing, supporting the general view that mahogany does not rely upon seed bank dynamics for regeneration (Lamb 1966).

Juvenile recruitment

In contrast to vertebrate predation, juvenile recruitment differed significantly among the nested levels in the two microhabitats (ANOVA, $F_{(2,95)} = 6.04$, $P = 0.0041$) and, as predicted by the Janzen–Connell mechanism, was strongly distant-dependent (Fig. 4). We encountered almost twice as many live understory juveniles far from adults as opposed to near them (Tukey–Kramer pairwise test, $P = 0.0066$), and when compared to the gap zones, recruitment remained lowest near focal adults (Fig. 4). Lending further support to the mechanism was a highly significant and negative effect of adult density on juve-

Fig. 4 Proportion of seeds surviving to the juvenile stage (juvenile recruitment) in the trunk and crown zones of treefall gaps, and in the understory near and far away from adult mahoganies. Lowercase letters indicate significant differences at $P = 0.05$ among means using REGW multiple comparison test. Bars are means $\pm$ 1 SE
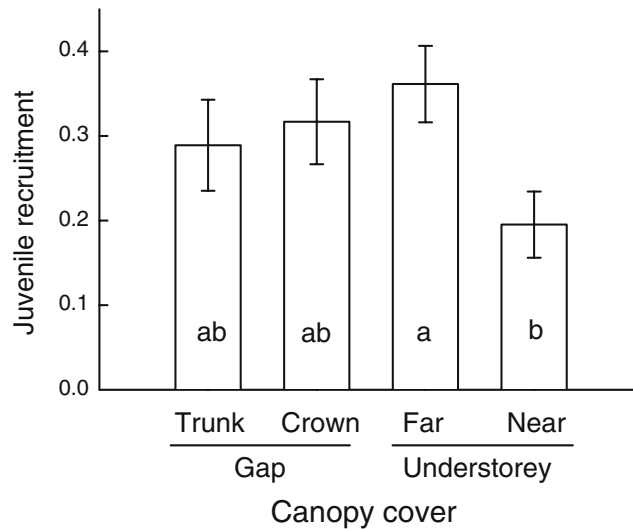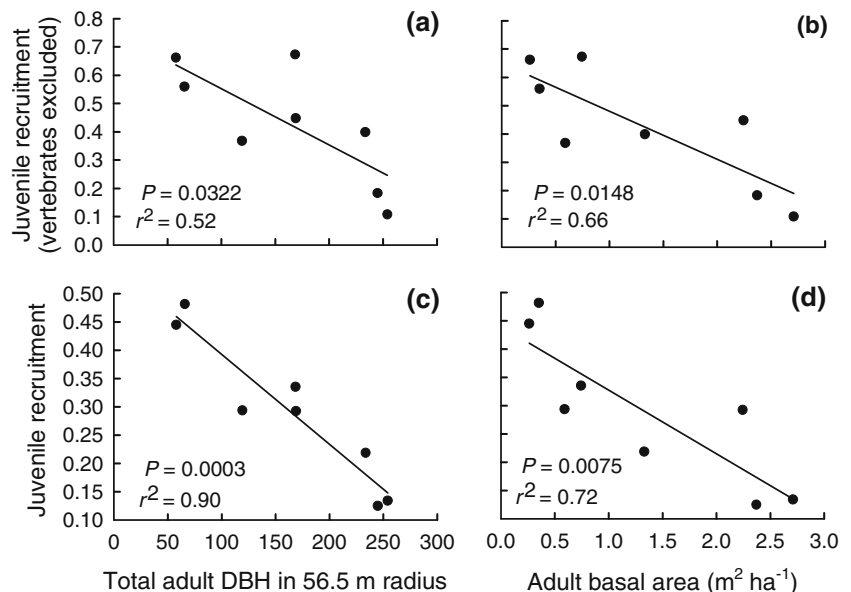

Fig. 5a–d The effect of adult density expressed as both basal area and summed DBH within a 1-ha circular area centred around each focal adult on mean proportion of seeds surviving to the juvenile stage (juvenile recruitment) in the absence of mammalian seed predators (i.e. in the no-access exclosures) (**a**, **b**) and overall juvenile recruitment (**c**, **d**) at eight mahogany adults

nile recruitment (ANOVA, $F_{(1,95)} = 36.61$, $P < 0.0001$): only half as many seeds survived to the juvenile stage around clumped adults as around isolated adults (mean proportion ± 1 SE: clumped 0.20 ± 0.049; isolated 0.038 ± 0.050). In fact, 27% of the plots at clumped adults had zero juvenile recruitment compared to only 4% at isolated adults.

The strongest evidence for density-dependent mortality was from plots excluding all vertebrates. In these plots, the proportion of live juveniles declined significantly as a function of both conspecific adult basal area ($r^2 = 0.66$, $n = 8$, $P = 0.015$) and summed adult DBH ($r^2 = 0.52$, $n = 8$, $P = 0.032$, Fig. 5a, b). Because seeds in these plots were protected from vertebrate predation, this indicates that the density-dependent recruitment was being driven by some post-germination factor(s),

either during course of seedling establishment and/or following establishment. Pooling all 12 plots per tree, we found that overall recruitment declined dramatically with increasing conspecific adult basal area ($n = 8$, $P = 0.0075$) and summed adult DBH ($n = 8$, $P = 0.0003$). Amazingly, summed adult DBH explained 90% of the variation in overall juvenile recruitment across the eight trees (adult basal area explained 72%; Fig. 5c, d).

The effect of the exclosure treatments on juvenile recruitment varied with microhabitat, as revealed by a significant interaction (ANOVA, $F_{(2,95)} = 4.25$, $P = 0.019$). Within gaps, there remained a strong positive effect of vertebrate exclusion on juvenile recruitment (Tukey–Kramer pairwise test, $P < 0.0005$), but in the shaded understory, juvenile recruitment was similar among the three exclosure treatments and no longer

enhanced by protection from small mammals ($P > 0.35$), suggesting the occurrence of a post-germination mortality factor that was specific to the understory.

Discussion

Seed predation

The exclosure experiments provided evidence that small mammals are a major post-dispersal predator of *S. macrophylla* seeds at the study site. These results are consistent with Grogan and Galvão (2006) who also concluded that seed predation by rodents was widespread and of greater magnitude than that by insects; however, they found a lower intensity of predation than us in their lightly logged forest fragment. Our findings, however, differ from those reported by Gullison et al. (1996), who reported that insect and fungal attack caused the mortality of 58% of seeds around five mahogany adults in Bolivia. Also, contrary to others (Schupp 1988; Schupp and Frost 1989) and recent findings by Grogan and Galvão (2006), but similar to a Neotropical tree (*Ocotea endresiana*) study by Wenny (2000), we found no differences in seed losses between understory and gap locations, although predation was slightly higher near clumped adults in gaps than in the understory ($P = 0.15$).

The likely agents responsible for the seed losses are spiny rats (*Proechimys* spp.), which are known to be important seed predators in Neotropical forests (Wright et al. 2000) and at the site (Lambert 2004). A limitation in this study was our inability to determine the ultimate fates of seeds that may have been removed intact and cached by rodents (Hoch and Adler 1997). Elsewhere in Pará, a *Proechimys* individual was filmed carrying away a *S. macrophylla* seed; however, this event was infrequent (0.03%) (T. Clements, unpublished data). Recently, Lambert et al. (2005), working at Pinkatí as well, found that the biomass of *Proecymis* spp. at the site was positively correlated with rates of mahogany and peanut seed removal.

We found little evidence that seed predators preferentially attacked *S. macrophylla* seeds nearest to the tree. Similarly, no evidence of distant-dependent predation of mahogany seeds was detected at ten heavily fruiting, isolated trees by Grogan and Galvão (2006). The most plausible explanation for the lack of a distance effect is that, unlike many invertebrate seed predators (e.g. Janzen 1971, 1980; Howe et al. 1985), rodents are relatively unspecialized in their diet and foraging activities (Hammond and Brown 1998). Numerous other studies have confirmed the general conclusion that post-dispersal seed predation by vertebrates is not distant-dependent (reviewed in Hammond and Brown 1998, but see Schupp 1988, and recently, Wyatt and Silman 2004).

Yet, at a larger spatial scale, we found evidence suggesting density-dependent attack: more seeds were predated in treefall gaps near clumped fruiting adults than in those near isolated adults (see Fig. 2). While canopy gaps are clearly favourable to the growth and survival of mahogany juveniles (Grogan et al. 2003a; Negreros-Castillo et al. 2003; Grogan et al. 2005; J.M. Norghauer et al., in preparation), these results suggest that seeds arriving in gaps are at greater risk of vertebrate predation where seed shadows overlap and/or where seed densities are greater (sensu Schupp 1995). Unfortunately, most studies to date investigating seed predation in the context of the Janzen–Connell model have focused on isolated trees. Two studies that examined seed losses at varying adult densities used either an abundant subcanopy tree (Schupp 1992) or a common palm species (Brewer and Webb 2001), and both reported positive density dependence presumably owing to predator satiation, whereas we found the opposite trend for the relatively rare mahogany. In Peru, Cintra (1997) also found a negative relationship between seed survival and the number of conspecific adults for the Amazonian tree *Dipteryx micrantha*, which emerged at relatively large spatial scales (200–400 ha).

This higher vertebrate predation at adult concentrations may in part be explained by the timing of dispersal and foraging behaviour of small mammals. It is well known that fruit production can vary enormously in markedly seasonal tropical forests (Howe and Smallwood 1982). Mahogany seed dispersal occurs during the dry season when resources are scarce relative to the wet season, with the result that small mammal predators may cue in on areas with greater seed availability during that season. Further, in any given year, there is a greater likelihood that in areas of clumped adults at least one tree will be fruiting. In addition, mahogany groves typically form in highly disturbed habitats, which may represent enhanced habitat quality for small mammals (Malcolm 1995; Beck 2002; Beck et al. 2004).

Juvenile recruitment

In contrast to the patterns of mahogany seed predation, we observed a strong, positive effect of dispersal distance on the proportion of seeds surviving as juveniles at both high and low adult densities, as predicted by the Janzen–Connell mechanism. Elsewhere in southern Pará, Grogan and Galvão (2006) also reported increased survivorship of juveniles far from parents (50 m) compared to close-by, although the effect was slight. Other Neotropical studies also have documented increasing seedling recruitment with distance from conspecifics (e.g. Clark and Clark 1984; Howe et al. 1985, reviewed in Turner 2001, recently Wyatt and Silman 2004). Recently, based on a meta-analysis of Janzen–Connell mechanism literature, Hyatt et al. (2003) concluded that increased survival away from parents is more prevalent for seedlings than for seed stages. Based on our results, we predict that the median dispersal distance of surviving mahogany juveniles

within a given cohort should increase with time since germination (Augspurger 1983).

Moreover, we also found a strong negative effect of local adult density on the recruitment of mahogany juveniles, suggesting that the factors driving distant-dependent mortality also operate at the population level. In order for density-dependent processes to promote the coexistence of tree species, progeny survival should be reduced where densities of conspecific adults are greatest (sensu Schupp 1992; Webb and Peart 1999). If the processes driving these density-dependent patterns are typical across years and mahogany populations, we conclude that the probability of juvenile recruitment, and hence the ability to experience a gap event necessary to attain reproductive maturity, is reduced near increasingly aggregated conspecific adults.

The disparity in juvenile recruitment between clumped and isolated adult areas could not be explained by vertebrate predation alone. When predation was controlled (by excluding all vertebrates), we still found a dramatic decline in the mean survivorship with increasing conspecific adult density (as measured by basal area and summed DBH, Fig. 5). Unfortunately, few comparable tropical studies have tracked the fate of progeny in the absence of seed predation to obtain a richer picture of post-dispersal dynamics (e.g. Asquith et al. 1997; Wenny 2000; Demattia et al. 2004). Our results imply that any survival advantage gained by mahogany seeds that successfully escape seed predation will be counter-balanced by post-germination mortality that intensifies with increasing conspecific adult size and densities. Moreover, a surprisingly high amount of the variation in overall juvenile recruitment at ten months (72–90%) was explained by measures of local conspecific adult size and density. Collectively, our findings suggest that distant- and density-dependent patterns in juvenile recruitment are driven by one or more post-germination factor(s) acting primarily during the seed-to-juvenile transition. We found many leafless and dead stems and stunted stems only 5–15 cm tall. Our results agree with Harms et al. (2000), who found a pervasive negative density dependence during the seed-to-seedling transition in a tropical forest community in Panama.

The most plausible explanation for this density-dependent effect on juvenile recruitment is host-specific invertebrate herbivory. Newly germinating mahogany seedlings are attacked by *S. poliophaea*, a microlepidopteran moth, which, because of its small size (ca. 1 cm), could have easily reached and oviposited on germinants in both the semi-access and no-access exclosures. Working elsewhere in Pará, Grogan (2001) concluded that "*S. poliophaea* was the principal cause of mortality at the four trees with highest initial seedling densities, particularly during the first growing season" (p. 219). In subsequent experimental work at Pinkaití, we also have found pervasive distant- and density-dependent damage and mortality to newly germinating seedlings by *S. poliophaea* caterpillars (J.M. Norghauer et al., in preparation).

Damping off pathogens also are known to cause mortality during the mahogany's seed-to-juvenile transition (Grogan et al. 2003b) and may have contributed to the patterns in recruitment observed here. In studies of other Neotropical trees, mortality caused by damping off pathogens declined with dispersal distance from the parent and was absent in canopy gaps (Augspurger 1984). Alternatively, or in possibly in conjunction with this, susceptibility to drought of mahogany juveniles (Gerhardt 1998; Grogan et al. 2003a) may be greater in areas where adults are clumped, although this seems unlikely as we visited plots early into the dry season and drought alone thus fails to account for the strong distance effect that we observed in survivorship at the scale of individual trees.

In conclusion, our study indicates that seed predation by small mammals is a major source of post-dispersal mortality of mahogany seeds and is more concentrated in gaps at clumped than isolated fruiting adults, but is not reduced by dispersal distance, providing only partial support for the Janzen–Connell mechanism. In contrast, additional mortality in the seed-to-juvenile transition was unmistakably negatively correlated with distance and also increased at clumped adults. This result suggests a strong selective advantage for dispersal away from the parent tree in mahogany, especially in the shaded understory, and supports the Janzen–Connell mechanism. We predict that the probability of recruitment of mahogany adults will be reduced at clumped compared to isolated parents, and that long-distance dispersal events should increase in relative importance at conspecific adult aggregations, and especially downwind (W–NW) of them.

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