The Importance of Tree Size and Fecundity for Wind Dispersal of Big-Leaf Mahogany

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Abstract

Seed dispersal by wind is a critical yet poorly understood process in tropical forest trees. How tree size and fecundity affect this process at the population level remains largely unknown because of insufficient replication across adults. We measured seed dispersal by the endangered neotropical timber species big-leaf mahogany (Swietenia macrophylla King, Meliaceae) in the Brazilian Amazon at 25 relatively isolated trees using multiple 1-m wide belt transects extended 100 m downwind. Tree diameter and fecundity correlated positively with increased seed shadow extent; but in combination large, high fecundity trees contributed disproportionately to longer-distance dispersal events (>60 m). Among three empirical models fitted to seed density vs. distance in one dimension, the Student-t (2Dt) generally fit best (compared to the negative exponential and inverse power). When seedfall downwind was modelled in two dimensions using a normalised sample, it peaked furthest downwind (c. 25 m) for large, high-fecundity trees; with the inverse Gaussian and Weibull functions providing comparable fits that were slightly better than the lognormal. Although most seeds fell within 30 m of parent trees, relatively few juveniles were found within this distance, resulting in juvenile-to-seed ratios peaking at c. 35–45 m. Using the 2Dt model fits to predict seed densities downwind, coupled with known fecundity data for 2000–2009, we evaluated potential Swietenia regeneration near adults (≤30 m dispersal) and beyond 30 m. Mean seed arrival into canopy gaps >30 m downwind was more than 3× greater for large, high fecundity trees than small, high-fecundity trees. Tree seed production did not necessarily scale up proportionately with diameter, and was not consistent across years, and this resulting intraspecific variation can have important consequences for local patterns of dispersal in forests. Our results have important implications for management and conservation of big-leaf mahogany populations, and may apply to other threatened wind-dispersed Meliaceae trees.

Citation: Norghauer JM, Nock CA, Grogan J (2011) The Importance of Tree Size and Fecundity for Wind Dispersal of Big-Leaf Mahogany. PLoS ONE 6(3): e17488. doi:10.1371/journal.pone.0017488

Editor: Andrew Hector, University of Zurich, Switzerland

Received August 27, 2010; Accepted February 7, 2011; Published March 7, 2011

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Funding: This study was partly funded by a Grant for Graduate Research Abroad from OAS (Organisation of American States) to JMN, and from the USDA Forest Service’s International Institute of Tropical Forestry to JG. JMN is grateful for a University of Toronto Fellowship and V. J. Nordin Prize from the Faculty of Forestry. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Seed dispersal is a critical life phase for plants that plays a key role in driving the dynamics, distribution, and persistence of plant populations and communities [1–4]. This is especially true in tropical forests where most tree species are rare and thought to be severely seed limited [5–9]. Patterns of seed-fall set the stage for a suite of post-dispersal events that can affect recruitment rates, including seed predation and germination, herbivory and competition, resource use and acquisition, and overhead canopy disturbances [10–14]. Together, these events help structure tree population sizes and distributions, influencing the composition of adult forest trees at a given time and place [15–17,3].

Local negative density-dependence (NDD) in juvenile tree recruitment and mortality is not uncommon in tropical forests, but likely stronger and more common in the critical seed-to-seedling and seedling-to-sapling stages (i.e., <1-cm stem diameter) [18,19]. This NDD process is directly linked to the dispersal process because seeds dispersed relatively far should gain a fitness advantage by becoming locally rare [10,11,13]. Excellent empirical work has begun to examine interspecific variation in dispersal of forest trees [20–23], but less explored is intraspecific variation at the population level, especially for wind-dispersed trees representing c. 10–25% of species in these forests [6]. From both a conservation and management perspective, such research takes on greater urgency for threatened timber tree species.

A case in point is big-leaf mahogany, Swietenia macrophylla King (Meliaceae, henceforth ‘mahogany’), a high-value neotropical timber species that is both wind dispersed and threatened by overexploitation and deforestation [24]. This species has long been an iconic symbol at the nexus of sustainable forest management and conservation; it is on both IUCN’s Red-List and CITES Appendix II because of regeneration failure and population declines after logging [25].

Tree regeneration can fail because of source disruptions to seed dispersal, which in turn can impact other ecological processes [3]. For timber species, the overriding disruption occurs via reductions in the seed source through removal of reproductive trees from the population. In the case of mahogany and related high-value Meliaceae, rampant logging has effectively ‘mined’ populations of large adult trees, exacerbating natural rarity in forests (<=1 adult trees ha⁻¹ at landscape scales; [26–29]). At this scale mahogany
Intraspecific Variation in Tree Seed Shadows

In this study we documented intraspecific variation in seed dispersal around 25 relatively isolated fruiting trees in a logged mahogany population in Pará, Brazil. We asked: (1) What is the relationship between tree traits, namely stem diameter and fecundity (seed crop size), and patterns of seed dispersal? (2) Which phenomenological model(s) best describes the relationship between distance and density of dispersed seeds? (3) What is the relationship of already established mahogany seedlings to observed seed-fall patterns? (4) What are the possible consequences of dispersal variation for spatial patterns of adult recruitment? We end by considering the implications of (1) – (4) for management and conservation of this rare and threatened tree species and related genera. As far as we know, this sample size is among the largest for describing seed dispersal of any forest tree.

Methods

Study species

Big-leaf mahogany is a canopy-emergent tree sometimes exceeding 50 m height and 2 m diameter with an extensive natural range from Mexico to Bolivia [26]. Adult trees are monoecious with reproductive onset from c. 20–30 cm diam, though fruit production is rare <30 cm diam [27,30,31]. Fruit production is annual or supra-annual. Woody fruit capsules are 9–19 cm in length and contain c. 40–42 viable seeds per fruit [31]. Seeds are large for a wind-dispersed species (mean wet/dry weight = 0.56 g/0.37 g) and encased in 5–13 cm long cinnamon-coloured, winged samaroid diaspores that are conspicuous in the leaf litter layer [31]. In the southeastern Amazon region, mahogany seeds disperse during the early to mid dry season; dispersal is nearly complete by early September, and is strongly skewed to the west of parent trees by prevailing dry-season winds [31,37]. Similar results have been reported from Mexico [38]. Seeds lack a dormancy mechanism; germination is triggered by moisture imbibition during the early wet season months [31].

Study site

Our study was conducted in a 704-ha area within a larger forest fragment (4100 ha) called Marajoara (7°50’S, 50°16’W) located in southeast Pará state, 34 km northwest of Redenção. This forest was selectively logged in 1992–1994 for mahogany, reducing landscape-scale density from 0.65 to 0.19 trees >20 cm diam ha−1 [28]. Forest vegetation is semi-evergreen with a deciduous component. Climate is tropical dry and strongly seasonal, with rains (c. 1600–2100 yr−1) falling primarily between September and May [39].

Measuring seed dispersal

On 13–14 August 2005 we selected 25 mahogany trees >30 cm diam within the study area that had completed seed dispersal or were near completion — that is, dehisced fruit capsules in the crown appeared almost bare. These trees were selected to maximise interspersion across the study area; all mahogany trees were separated from all fruiting or non-fruiting live conspecific trees by at least 125 m. During the next two weeks, six 1-m wide belt transects were established at 60° intervals radiating out from the base of each tree on the following bearings: NE (30°), E (90°), SE (150°), SW (210°), W (270°), and NW (330°). Transects extended 100 m downwind of each tree (i.e., SW, W, and NW) but only 50 m upwind (i.e., NE, E, and SE) because few seeds were expected on the windward side [31]. All transects were carefully searched for mahogany seeds, first by examining the litter surface and then carefully sifting through the leaf litter. The number of intact or predated seeds per 5-m distance interval was noted. We
also noted the presence of live mahogany juveniles that established in the previous year (2004) or earlier (any stems c. 10–20 cm tall and upwards) in each 5-m interval and recorded stem height to the nearest cm.

We used multiple transects because it was impractical to thoroughly search ‘wedges’ at so many trees (n = 25) needed to investigate variation in dispersal at the population level. Wedges that sample a constant proportion of the annulus with increasing distance reduce the risk of underestimating dispersal events at far distances (the tail). However, Skarpaas et al. [40] showed that when the prevailing direction of dispersal is already known, radial transects of a fixed width can describe the true seed shadow just as well as sampling in wedges.

Lateral tree crown extensions were estimated for each sampled tree by moving along each of the six bearings measuring the distance at which the overhead crown edge was perpendicular to the ground. For a given tree, the end-points of the crown extensions were connected with straight lines to form a six-sided polygon and the six triangles therein were summed to estimate the crown cross-sectional area (m²). We already knew that mahogany’s cross-sectional crown area increases exponentially with tree diameter, whereas height to the base of the crown increases linearly with diameter (see Grogan 2001 cited in [31]).

**Measuring tree seed crops**

To directly measure tree-level seed production (henceforth ‘fecundity’), two separate observers counted fruit capsules within the crown of each sampled tree. Mahogany’s large woody fruit capsules are readily identifiable in the crown from the ground during the mid to late dry season when crowns are leafless or nearly so. Each capsule consists of five pericarps that break apart and drop off in the dry season to expose the winged diaspores. To verify these tree-level fruit counts, fallen dehisced capsule pericarps (5 = 1 fruit) were collected beneath the crown area of each fruiting tree and the total count divided by five. The final capsule count used in analyses as a measure of individual tree fecundity was the larger figure yielded by the two methods (Fig. 1). This fecundity value estimated source strength (number of seeds released) in analyses.

**Tree seed crops estimated from transects**

For each 5-m annulus, total seed counts in the six radial transects were converted to seed density (m⁻²) by dividing by 30 m² (assuming no seeds landed further than sampled distances on upwind transects [31]) and multiplied by 1/3 the annulus area to obtain seed count per annulus. These new counts were summed over the 20 annuli to yield an estimate of tree seed production. The 1/3 correction corresponds to the 120° (out of 360°) downwind arc where most seeds fall during dispersal because of strong anisotropy. The key assumption in this calculation is that lateral tree crown extensions were estimated for each sampled tree by moving along each of the six bearings measuring the distance at which the overhead crown edge was perpendicular to the ground. For a given tree, the end-points of the crown extensions were connected with straight lines to form a six-sided polygon and the six triangles therein were summed to estimate the crown cross-sectional area (m²). We already knew that mahogany’s cross-sectional crown area increases exponentially with tree diameter, whereas height to the base of the crown increases linearly with diameter (see Grogan 2001 cited in [31]).

Figure 1. Fruit production as a function of stem diameter for 25 mahogany (*Swietenia macrophylla*) trees in 2005 in Pará, Brazil. One fruit capsule contains on average 40–42 viable seeds. The regression line was significant (adj. \( r^2 = 0.26, P = 0.0058, y = –17.1 + 0.775x \)) but lacked constant variance. The arrow points to a heavy fruiter outside 95% confidence intervals; its removal from the analysis resulted in a marginally significant relationship between tree diam and fruit production (adj. \( r^2 = 0.13, P = 0.047 \)). The inset shows the same 25 trees with diam and reproductive output log-transformed to stabilise the variance (adj. \( r^2 = 0.14, P = 0.0607 \)).

doi:10.1371/journal.pone.0017488.g001

In this equation, \( A \) is the trap area; \( Q \) is the number of seeds released, or source strength; \( r \) is the radial distance, and \( f(r) \) is the dispersal model (1/m²) described by equations listed in Table 1. In our mahogany study, \( A \) is the always same ‘trap’ area of 15 m²

\[
c = A \times s = A \times Q \times f(r)
\]
Table 1. Empirical models tested for mahogany (*Swietenia macrophylla*) seed dispersal expressed in one dimension and two dimensions downwind of 25 isolated trees at the Marajoira forest in Pará, Brazil.

| Function | Equation |
|----------|----------|
| **One-dimensional fitting**<sup>1</sup> | | |
| NE | \(a \exp(-br)\) |
| IP | \(ar^{-b}\) |
| 2D<sup>2</sup> | \((a/\pi b)(1 + r^2/b^2)^{-1}\) |
| **Two-dimensional fitting**<sup>3</sup> | | |
| LN<sup>4</sup> | \((ar[2\pi]^{0.5})^{-1}\exp\left(-((\pi r-b)/a)^2/2\right)\) |
| IG<sup>5</sup> | \((a/[2\pi r])^{0.5}\exp\left(-a(r-b)^2/2b^2\right)\) |
| WB<sup>6</sup> | \(ab^{-a}r^{-b-1}\exp\left(-r/b^2\right)\) |

\(r\) is the distance from the stem of the source tree.

1. Cousens et al. [4] (see Table 5.2 therein).
2. See Clark et al. 1999 [20].
3. Cousens et al. [4] (see Table 5.1 therein).
4. See Greene et al. 2004 [21].
5. See reference of Whelan 1988 in [4]; this is not the modified Wald equation by Katul et al. 2005 in which both parameters are estimated from wind speed and plant attributes.
6. See Higgins & Richardson 1999 in [4]; also see [21] and [33].

Statistical methods

We used one-way analysis of variance (ANOVA) to compare tree traits across the four size-fecundity groups. Three of the four dependent variables were transformed to stabilize variances and normalise model residuals. Specifically, both the number of fruit capsules and tree crown area were log-transformed, whereas tree crown area to diameter ratio was square-root transformed. One-way non-parametric analyses (Kruskal-Wallis tests) were used to compare patterns of seedfall among the four tree groups because neither log nor arcsine-square transformations met ANOVA assumptions based on visual inspection of the residuals against predicted variables.

We used the maximum likelihood method and default Nelder-Mead algorithm in the ‘mle2’ function of R (package ‘bbmle’ [44]) to estimate parameter values when fitting the three one-dimensional functions to the seed density vs. distance data for each of the four tree groups (SF, SM, LF, LM). A Poisson error distribution was assumed for seed counts following studies of other wind-dispersed tree species [20,21,33,40–43]. Models were evaluated using the negative log-likelihood (–ln L) and Akaike’s Information Criteria (AIC); for each the lowest value indicated the best overall fit. The above was also used for the normalised seed counts modelled in two dimensions.

Stepwise multiple linear regressions using a backward elimination process were performed to determine which tree traits best predicted total number of seeds downwind and their mean dispersal distances, and to gauge seed shadow extent and total number of seeds exceeding 60 m distance downwind (SW, W, NW). Dependent variables were based on a normalised sample (see above scaling factor) in two dimensions to estimate overall seed counts had a constant proportion of annulus been sampled instead of a diminishing one with distance. In these analyses, to satisfy model assumptions, all dependent variables were log-transformed as were the predictors tree crown area and total number of fruit capsules, whereas tree diameter and height were not. Model residuals and final model predictor variables were examined visually for heteroscedasticity and for collinearity using tolerance values and variance inflation factors (i.e., VIF = 1/tolerance); tolerance values <0.1 and VIFs >10 point to strong collinearity [45].

To avoid pseudo-replication, the heights of multiple juveniles found in the same 1-m ×5-m segment of a radial transect were first averaged prior to analyses. The relationship between patterns in seedfall and juveniles downwind of trees was investigated using the mean ratio of juveniles to seeds across the 25 trees. The number of juveniles across the SW, W, and NW transects were averaged on a per tree basis, as were the number of seeds in a given distance.
interval, based on their normalised counts (see above for ‘scaling factor’ used). Beyond 65 m, however, the total sample sizes from transect sampling became very small and thus prone to disproportionately greater error when scaled upwards (6–23 seeds per distance, and 8 juveniles only). For this reason we omitted data at these farthest distances. We fit a Loess smoother (parameter = 0.3) to explore possible changes in recruitment with ontogeny because it is more robust to this declining precision of the ratio with increasing distance from the source tree [43].

Estimating seed arrival in gaps near and far from trees
Seed densities per distance predicted by 2Dt (for LF, SF and LM, SM respectively) were converted into proportions of total seed crop in a 120° arc downwind. To estimate seed abundance near (≤30 m) and beyond >30 m downwind, the proportions of seed per downwind annulus segment were multiplied by each tree’s actual seed crop for a given year (2000–2009, see Supporting Information S1) assuming 40 viable seeds per fruit capsule. These seed abundances were then averaged across sampled trees on a yearly basis for each of the four size-fecundity groups, and each multiplied by the forest area (4%) likely in a ‘gap-like’ state when or soon after dispersal occurred. In the 1996–1997 wet season 2.6% of 16.5 km of trails at the site had new gaps formed because of tree- and branch-falls (<2 m tall vegetation, see [39] for details). Because the majority of these newly formed gaps do not fill in with vegetation within a year’s time, we assumed that half (1.3%) might be suitable for mahogany growth in the next year (a reasonable assumption in our experience, 1.3% + 2.6% = ~4%).

Results
Dispersal pattern
We found 5154 winged diaspores (hereafter, seeds) in transects around 25 mahogany trees (Table 2). Of these, 3622 seeds (70.3%) were found in 100-m long downwind transects west of parent trees (SW: 19.8%, W: 27.8%, NW: 22.7%), and 1521 seeds (29.7%) were found in upwind transects east of parent trees. Of these upwind seeds 78% were found within 10 m of the tree trunk, with hardly any landing beyond 20 m. Downwind seeds were located in different distance classes, with a peak count of 62 seeds (12.4 seeds m\(^{-2}\)) in a NW transect at 0.5 m distance. At four trees searched beyond 100 m, the maximum distance travelled by a found seed was 155 m. This occurred in the W transect of the tree with the highest fruit production (122 capsules).

Dispersal patterns across tree groups
Sampled trees differed greatly by individual size and fecundity (Table 3). Tree diameters ranged threefold, from 32–99 cm diam. Estimated tree crown areas ranged 15-fold, from 37–612 m\(^2\), while fruit crop size ranged from 2–122 capsules. Differences in crown area and the ratio of crown area to diameter were not as pronounced, with SM and LF trees sharing similar values. Crown area was positively correlated with tree heights (Pearson \(r = 0.74\); missing heights for 10 of 25 trees were interpolated).

In transects, we found three times as many seeds around trees producing many (M) vs. few (F) fruit, irrespective of tree size, and these more fecund trees had more seeds dispersed downwind as well (Table 2). While >50% of transect seeds were found within 15 m of tree stems for all tree groups, in terms of total estimated seed crop, on average, the lowest percentage (19%) of seeds dispersed within a 15-m radius was observed at large trees producing many fruits (LM). A significantly higher proportion of LM seeds landed 50–100 m downwind compared to the other three groups (Figs. 2, 3). In sum, SM, SF, and LF showed relatively similar seed dispersal patterns compared to LM trees, which spread seeds out more and attained longer dispersal distances (Figs. 2, 3).

Evaluation of dispersal functions
The 2Dt provided the best overall fit for dispersal of small trees irrespective of fecundity (SF, SM), and for large trees with few fruits (LF). For LM trees the 2Dt also fit reasonably well, but not as well as the NE function. The IP consistently fit poorly for all four combinations of tree size and fecundity. The predicted 2Dt curve of LM trees was different from the SM, LF, and SF trees in having a longer tail (Table 4); the latter two were very similar for all functions fitted (Fig. 2). Similar results — namely the broader, ‘fatter-tailed’ seed shadow of LM — were found when dispersal was expressed as the relative frequency of dispersal distances occurring, and modelled as a pdf using LN (lognormal), IG (inverse Gaussian) and WB (Wright bulb) fitted functions (Fig. 3). Compared to Fig. 2, modelling dispersal in two-dimensions made LF, SF, and SM dispersal patterns more similar, with a peak now revealed in seedfall beginning at c. 5–10 m from the tree base, but furthest in LM trees at c. 25 m. The IG and WB fit comparably well, and slightly better than LN, for this species at the site.

Long-distance dispersal (LDD)
We found 40 mahogany seeds 100–160 m downwind of four LM trees (8, 7, 9, and 16 seeds tree\(^{-1}\) in a pooled sampled area of 2160 m\(^2\), equivalent to 0.0185 seeds m\(^{-2}\). We occasionally came across multiple seeds (2–4) in the same 3-m \(\times\) 3-m quadrat, or clumped among two consecutive quadrats along transects, likely carried there together by strong uplifting winds [31,46].

Multiple step-wise regression analyses showed that none of the four traits significantly predicted mean seed dispersal distance downwind, except for possibly tree crown area at a less stringent \(\alpha = 0.10\) (\(P = 0.086\); model \(F_{1,23} = 3.22, R^2 = 0.12\)). However, the number of fruit capsules (\(P<0.0001\)), and to a lesser extent, crown area (\(P = 0.0034\), explained 87% of variation in the total number of seeds landing downwind of mahogany trees (model \(F_{2,23} = 72.4, R^2 = 0.87\)). Similarly, the number of seeds that exceeded 60 m distance – a proxy for seed shadow extent – was best predicted by number of fruit capsules (\(P = 0.0007\) and crown area (\(P = 0.024\) (model \(F_{2,25} = 17.3, R^2 = 0.61\)). Neither tree height nor diameter was a significant predictor in the three models (all six P values = 0.35–0.98).

Comparing seed distributions to existing juveniles
A total of 82 mahogany juvenile stems were found in 11150 m\(^2\) around 23 adult trees. Not a single large juvenile (>50 cm tall) was found beneath the canopy of any sampled tree; the largest juvenile encountered was 80 cm tall, 70 m downwind of a small (50 cm diam) tree. Only 4 juveniles were found more than 15 m from any parent on upwind transects (NE, E, SW; total upwind = 16). Of the 66 juveniles at downwind distances, 18%, 48%, and 33% of them were found in SW, W, and NW directions, respectively. Mean log-transformed heights (± SE) of juveniles were significantly different among distance classes (one-way ANOVA, \(F_{2,65} = 4.13, P = 0.0201\). Juveniles farther away (50–100 m) were significantly taller (~25% more) than juveniles within 50 m of parent trees (means for respective distance classes: 0–15 m, 28.5 ± 1.9 cm; 15–50 m: 31.0 ± 2.1 cm; 50–100 m: 41.5 ± 2.5 cm). The ‘repulsion effect’ of parent trees on offspring, defined here as the juvenile-to-seed ratio, increased with dispersal distance and peaked at 35–50 m (Fig. 4).
Table 2. Seed dispersal patterns of mahogany (Swietenia macrophylla) trees (n = 25) at the Marajoara forest in Pará, Brazil.

| Tree group | n | Total no. seeds found | No. seeds | Estimated total seed crop per tree | Proportion of estimated total seed crop per tree | No. seeds >50 m in transects |
|------------|---|-----------------------|-----------|-----------------------------------|-----------------------------------------------|-----------------------------|
| SF         | 8 | 91±24                 | 30±12     | 60±13                            | 362±70                                        | 0.38±0.06                   | 0.45±0.05                   | 0.17±0.06                   | 69±24                       |
| SM         | 5 | 306±57                | 118±27    | 188±46                           | 1067±159                                      | 0.47±0.09                    | 0.39±0.06                   | 0.14±0.05                   | 155±54                      |
| LF         | 5 | 97±33                 | 44±32     | 53±4                             | 445±95                                        | 0.33±0.07                    | 0.40±0.03                   | 0.26±0.08                   | 97±37                       |
| LM         | 7 | 345±98                | 68±23     | 276±76                           | 2263±554                                      | 0.19±0.03                    | 0.56±0.01                   | 0.25±0.02                   | 542±107                     |

Notes: The categories are combinations of small vs. large tree sizes (30–60 cm vs. 60–100 cm diam, respectively) with few vs. many fruits produced (≤15 capsules vs. >15 capsules, respectively [size-fecundity classes: SF = small–few, SM = small–many, LF = large–few, LM = large–many]). Values presented are means ± (1 SE). Within column comparisons across tree groups were made using Kruskal-Wallis tests (df = 3).

Potential regeneration near and far from trees

For the size-fecundity groups SF, LF, SM, and LM the mean total seed inputs ≤30 m downwind, in a 120° arc, ranged from 49–218, 39–130, 443–1189, and 171–1976 seeds per year, respectively. However, seed arrivals into canopy gaps beyond 30 m, where adult recruitment is more likely ([Fig. 4]), was more than 3x greater for LM than SM, with both groups exceeding inputs downwind generated by SF and LF trees ([Fig. 5]).

Discussion

Mahogany’s seed shadow

Most big-leaf mahogany seeds dispersed to the west or downwind, yet the bulk of them landed beneath or near crowns (<30 m). This result agrees with two previous studies of 6 and 11 heavily fruiting big-leaf mahogany adults, at Marajoara and in Mexico, respectively [31,39], but not in a Bolivian forest [27] nor for the closely related Entandrophragma spp. (African mahogany) [47]. This anisotropic dispersal was highly predictable despite wide variation in crown areas and branching patterns. The most plausible explanation is that, coupled with mahogany’s emergent position above a low irregular canopy, pervasive, strong local dry season winds generate this pattern each year. Similar skewed seed deposition patterns were observed for Lonchocarpus pentaphylus (n = 1) and Tachigalia ceratocarpa (n = 2) trees in a Panamanian forest [48,49]. Whether local winds skew dispersal in temperate forest stands remains less certain because most dispersal studies assume a symmetric two-dimensional kernel when model fitting, which is increasingly questionable for wind-dispersed species [6,50]. Nonetheless, many studies of dispersal in temperate stands confirm the general impression of very localized seedfall (irrespective of vector), except for perhaps the smallest-seeded species [16,20,21,51]. In tropical forests, where stands are more mixed and structurally diverse, a steep decline of seed density with distance from the parent tree is the norm rather than the exception [1,13,17,22,23].

Table 3. Tree characteristics of mahogany (Swietenia macrophylla) trees grouped into four size-fecundity classes at the Marajoara forest in Pará, Brazil.

| Variables                  | F.3, 24 | SF (n = 8) | SM (n = 5) | LF (n = 5) | LM (n = 7) |
|----------------------------|---------|------------|------------|------------|------------|
| Diameter (cm)              | 21.29** | 41.8±2.3a  | 48.7±5.2a  | 74.4±5.9b  | 82.5±4.9b  |
| No. capsules†              | 17.05** | 10.1±1.6a  | 40.6±7.1b  | 6.8±1.3a   | 63.1±12.7b |
| Height (m)                 | 17.77** | 21.8±0.6b  | 24.0±0.7a  | 27.6±1.2a  | 28.1±0.7a  |
| Crown area (m²) †          | 14.32** | 59.0±6.7a  | 95.0±26.4bc| 157±10.2bc | 253±48.9a  |
| Crown area: diam †         | 4.47*   | 1.40±0.17a | 1.91±0.48ab| 2.15±0.18ab| 3.07±0.55b |

Notes: Means (± SE) with different letters are significantly different at α = 0.05 following post-hoc Tukey HSD tests (size-fecundity classes: SF = small diam–few fruits, SM = small diam–many fruits, LF = large diam–few fruits, LM = large diam–many fruits). One-way ANOVA model significance:
† P < 0.0001;
‡ P = 0.0141.
 Measured in 2005.
θ Height to the base of the live crown; measured in 1998 on 15 of the 25 trees, with other 10 interpolated using regression of height vs. diam (n = 153 trees).
* log-transformed variable for ANOVA.
** square-root transformed variable for ANOVA.
across 10 years (Fig. 1, Supporting Information S1). In a given year only a few trees will have large seed crops, and some skip reproduction altogether. Large successive crops of fruit on the same tree are rare, a pattern likely for many other tropical trees in other forests as well [34,35,51–55]. In an African rain forest, fecundity was poorly explained by individual tree traits like crown area, height and diameter for nine species including three that were wind-dispersed [22]. Elsewhere, diameter was a significant yet imprecise ($r^2 = 0.26$) predictor of tree-level fecundity in only 8 of 14 tree species in a Malaysian rain forest [56]. Hence the generality of using a positive scaling of diameter with fecundity deserves greater scrutiny when modeling dispersal within a species if tree size-fecundity relationships tend to flatten beyond a reproductive size-threshold [51].

Small mahogany trees with many fruits (SM) cast a slightly broader seed shadow than did large trees with few fruits (LF), but both were eclipsed by large trees bearing many fruits (LM; Figs. 2, 3, Table 4). This suggests that producing more fruits is more effective to a parent for dispersal than being large, all else being equal. More seeds in the tree’s crown, positioned at more release points, should increase the probability of catching stronger than average uplifting winds needed for extended downwind dispersal (>50 m, Table 3), and especially turbulent wind flows needed to travel very far (LDD) [46]. This effect is further amplified by having a broader crown in LM trees. This interpretation of a synergism between a larger tree size and a larger seed crop was supported by the results of the two-dimensional model fitting of a distance pdf to the data (Fig. 3), which should have removed any
fecundity influence on dispersal. For example, in a temperate forest, interspecific dispersal distance was positively correlated with estimates of fecundity for 14 canopy tree species [16]. An interesting, largely unexplored issue is whether ontogenetic shifts occur in allocation to reproduction in mahogany (Norghauer, pos. obs.) or other tree species, towards producing more smaller sized seeds on average so as to increase overall size of the fruit crop, and thereby gain a potential dispersal advantage.

**Figure 3.** Dispersal of mahogany (*Swietenia macrophylla*) seeds in two dimensions downwind of 25 parent trees in Para´, Brazil. Relative frequency of dispersal is the proportions of normalised seed counts downwind per tree for a given 5-m distance interval, generated from the original 1-m wide transects. The probability density function (pdf) of a given distance interval occurring was fitted to the normalised data using three equations: IG = inverse Gaussian (Wald); LN = lognormal; and WB = Weibull (see **Table 1**). doi:10.1371/journal.pone.0017488.g003

**Table 4.** Estimated parameters and fit statistics of empirical dispersal models for 25 mahogany (*Swietenia macrophylla*) trees at the Marajoara forest, Pará, Brazil.

| Tree group       | One-dimensional model fitting | Two-dimensional model fitting |
|------------------|--------------------------------|--------------------------------|
|                  | Function | a     | b     | -ln L | AIC   | Function | a     | b     | -ln L | AIC   |
| Small–few (SF)   | IP       | 0.012 | 1.069 | 335.8 | 675.6 | LN       | 1.062 | 3.206 | 34.7  | 73.4  |
|                  | NE       | 0.002 | 0.553 | 290.0 | 584.1 | IG       | 43.650| 32.343| 32.4  | 68.8  |
|                  | 2Dt      | 1.050 | 92.635| 287.2 | 578.3 | WB       | 1.462 | 35.228| 32.6  | 69.1  |
| Small–many (SM)  | IP       | 0.010 | 1.101 | 447.7 | 899.5 | LN       | 1.086 | 3.185 | 21.6  | 47.2  |
|                  | NE       | 0.003 | 0.077 | 336.9 | 677.8 | IG       | 41.230| 32.128| 20.2  | 44.3  |
|                  | 2Dt      | 1.291 | 149.940| 327.4 | 658.8 | WB       | 1.415 | 34.800| 20.2  | 44.3  |
| Large–few (LF)   | IP       | 0.014 | 1.032 | 188.0 | 380.0 | LN       | 1.194 | 3.298 | 22.6  | 49.2  |
|                  | NE       | 0.004 | 0.064 | 175.5 | 354.9 | IG       | 38.349| 37.848| 21.1  | 46.3  |
|                  | 2Dt      | 0.871 | 57.328| 167.5 | 338.9 | WB       | 1.343 | 40.282| 21.2  | 46.4  |
| Large–many (LM)  | IP       | 0.004 | 0.766 | 878.7 | 1761.5| LN       | 0.918 | 3.512 | 31.1  | 66.2  |
|                  | NE       | 0.002 | 0.047 | 554.6 | 1113.2| IG       | 77.146| 40.796| 29.2  | 62.3  |
|                  | 2Dt      | 0.843 | 174.179| 601.0 | 1206.0| WB       | 1.804 | 45.293| 29.0  | 62.0  |

Better-fitting models indicated in bold.

Notes: Tree groups are factorial combinations of small vs. large tree size (30–60 cm vs. 60–100 cm diam, respectively) and few vs. many fruits (≤15 capsules vs. >15 capsules, respectively). Differences in AIC greater than 2 indicate little evidence in support of competing/alternative models. See Table 1 for equations describing the dispersal functions.

doi:10.1371/journal.pone.0017488.t004
Tree height versus crown area influence on dispersal patterns

Tree crown area better explained the variation in seed dispersal than height. Tree height variation may be more important in wetter forests [57] with taller canopies than for the emergent mahogany, whose crowns are generally well exposed to winds once a reproductive diameter is reached [31] (Norghauer, pers. observ.). Nevertheless, tree height may matter more for explaining dispersal differences between species and life forms. For example, it was a positive factor explaining dispersal distances among nine wind-dispersed species in Panama, and all species in general [23].

Another advantage to using crown area instead of tree height is that it accounts for reductions in leaf area due to senescence or limb breakage caused by falling neighbours. Trees with a higher ratio of crown area to diameter may have more photosynthate and other resources left over after maintenance costs to invest in reproduction [34,53]. This may partly explain the greater contribution of crown area as a strong predictor of mahogany’s seed shadow extent across the 25 isolated trees.

Modelling dispersal

Evaluating several dispersal functions was necessary because these mathematical constructions behave differently across dispersal distances. Overall the Student-t (2Dt) function fit best for three of the four size-fecundity groups. Compared to NE and IP, the 2Dt is more flexible at modeling copious seedfall near the parent tree and diminishing events farther downwind [20]. From a conservation perspective, whether the seed shadow tail is “thin” or “fat” has important implications for population spread and recovery in suitable habitat patches, and migration rates under climate change [6,20]. For the wind-dispersed Pinus halpensis, the negative exponential (NE) consistently underestimated seed densities at <25 m distances, whereas the inverse power law did so at 25–50 m [51]. In our analysis, the inverse power (IP) behaved similarly but overestimated mahogany dispersal >50 m at trees with many fruits (LM, SM), while the negative exponential (NE) was an intermediate fit in all cases, except for LM. Elsewhere, in Mexico, the NE was deemed sufficient for describing seed dispersal downwind of small and large heavily fruiting trees, although a linear fit was better for adult trees ≥75 cm diam [38].

Another result is that the negative exponential function is a good fit for seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil. The NE was deemed sufficient for modelling seed dispersal downwind of 25 parent trees in Pará, Brazil.
This result was anticipated based on both observational and experimental work that showed a specialist defoliator, *Stemisidota poliophaea* (Lepidoptera: Noctuidae), targeting newly germinating seedlings near (<30 m) parent mahogany trees, and that seedling escape and survival is highest between 50–100 m from parent trees [37,61].

The long-sought linkage between seed dispersal and plant demography remains elusive and muddled [3,15]. But the Janzen-Connell model implicitly suggests such a linkage, because the distance at which PRC is most pronounced for a species should set a minimum intraspecific spacing for recruitment of one or possibly several adults. For this reason, LM individuals should contribute disproportionately to local population growth, as suggested by Fig. 5. This result reflects the reality that, in moving further downwind of parent trees, not only does the likelihood of escaping lethal attacks to new and established seedlings increase, but as the seed shadow broadens, so does the *total* area of disturbed forest in a gap-like state available for seed arrivals [12,62].

Detecting and quantifying long-distance dispersal (LDD) is challenging because it is considered a rare event [46]. Nevertheless, it remains crucial to investigate how fecundity affects the occurrence of LDD and how, in turn, LDD may affect rates of seed survival through later stages of development [14]. The seed density vs. distance relationship for LM suggests that fecundity is vital to LDD — an interpretation strengthened by the two-dimensional results (compare LM and LF panels) — and agrees with an earlier study at Marajoara in which a few seeds dispersed at least 250 m [31]. The latter is consistent with the results from our extended sampling 100–160 m downwind, which indicate that seed dispersal by individuals of this species may form a very long tail. Longer tailed and broader shadows are predicted for trees >100 cm diam, which were not available for sampling in this population. It is possible that we have underestimated dispersal events at farther distances because we did not sample a constant proportion of the annulus downwind of trees in the form of ‘wedges’. However, a trade-off was unavoidable between sampling search area and the number of replicate sources (n = 25 trees) needed to investigate population-level variation in seedfall patterns. We conclude LDD events are probably more common than is generally appreciated for mahogany, and that LDD seeds may enjoy a disproportionately high recruitment rate [39]. Because most remnant mahogany populations are missing their large, most fecund trees, LDD should take on greater importance in logged secondary forest than at unlogged sites. Finally, apart from ‘catching’ LDD events in real time, it is also vital to follow post-seed dispersal fate in terms of survival and mortality processes [3,14,15].

**Implications for conservation and management of mahogany populations**

We cannot hope to effectively manage and restore economically important tree populations if we do not understand how variation in their seed dispersal arises, as well as the consequences of this variation for long-term regeneration. This issue assumes greater importance in the context of distance or density-dependent responsive natural enemies. Yet many empirical studies of dispersal use too few individuals to capture realistic variation at the population level of canopy trees. The justification often given for focussing sampling efforts on trees with large seed crops is decreased measurement error [40]. On the contrary, we argue that unbiased sampling reflecting biological realism is necessary to effectively inform policy and planning. For example, individual trees with high fruit production are the minority in logged populations of mahogany [27,30,31] and probably for other timber and tropical tree species in both logged and unlogged forests [34,35,51–55]. The seed shadow will determine the potential area for early regeneration, and thus spatial limits to adult recruitment. A bias towards overestimating seed shadows is risked if these are inferred from studies of large, highly fecund individuals only and then applied to the rest of the population. In the present case, this would entail applying parameter estimates from NE (or IG and WB) models for LM trees to other size-fecundity groups which form the bulk of the population in any given year and place.

In Mexico and Central America, where the specialist mahogany seedling predator *Stemisidota poliophaea* has not been reported, concentrating post-harvesting silviculture in the near (<30 m) portion of the seed shadow has been advocated because this is where progeny are most abundant [38]. This management approach cannot be advocated in South America in light of results reported here. An alternative management scheme would be to locate advance regeneration and/or seed manually at far distances downwind, where escape from *S. poliophaea* herbivory is more likely, and where the broadened seed shadow covers more gaps; both factors should contribute to increased mahogany recruitment rates in logged forests [5,62]. Such measures take on the form of ‘strategic silviculture’, targeting the subset of the population in the best position to recruit into the canopy at minimal cost. A corollary is that large areas of forest are needed for sustained yield — but conservation benefits accrue because less land is converted to pasture or agriculture.

Sorely needed are annual observations of at least 10 yrs on *individual trees* [34,35] to provide minimally adequate records of inter-annual variation in fruit/seed production of tropical timber species. For related Meliaceae (e.g., *Cedrela, Khaya, Entandrophragma*), counts of capsules on bare crowns with binoculars, or of pericarps on the ground, is relatively straightforward. With this information in hand, foresters could identify and retain more consistent SM, but especially LM, trees during harvests, as the latter should contribute most to recruitment. Moreover, LM trees often have hollow boles anyway and thus are wasted once felled [28–30].

**Conclusions**

Using 25 reproductive big-leaf mahogany adults spanning the range in tree diameter and seed crops found in a selectively logged population, we examined tree-level factors shaping seed dispersal patterns. An increase in either tree size or its seed crop was sufficient to move more seeds further downwind of parents; but the seed shadow was largest and frequency of long-distance dispersal events was highest when these two traits were combined in large, high fecundity trees. Our results suggest a need for explicitly considering individual tree fecundity and both stem and crown size as possible traits influencing the shape and extent of a species’ seed shadow in forests.

**Supporting Information**

**Supporting Information S1** A table showing the annual fruit production of each of the 25 mahogany (*Swietenia macrophylla*) trees used in this study in 2000–2009, with brief notes. (PDF)

**Acknowledgments**

We are indebted to Nilson Vicente de Salles for his tireless help with seed sampling in the field. JMN thanks IMazon and the Marajoara field crew for their guidance and generous hospitality at the study site, Jay Malcolm for his encouragement and support, and Sean Thomas for early discussions.
and comments on a first draft of the manuscript. We are grateful for the instructive comments, criticisms and corrections suggested by two anonymous reviewers which significantly improved the original manuscript.

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Author Contributions

Conceived and designed the experiments: JMN. Performed the experiments: JMN. Analyzed the data: JMN CAN JG. Wrote the paper: JMN CAN JG.

PLoS ONE | www.plosone.org 11 March 2011 | Volume 6 | Issue 3 | e17488

Intraspecific Variation in Tree Seed Shadows
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