



## Predicting the terminal velocity of dipterocarp fruit

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### ABSTRACT

We measured the terminal velocity of helicopter-like fruit from the Dipterocarpaceae family and present a model predicting the terminal velocities for all dipterocarp species in the Malesiana region. A ballistic model of seed dispersal using the observed terminal velocities predicted dispersal distances of 17–77 m under normal atmospheric conditions. These data are of applied use in parametrizing models of species coexistence, forest regeneration and habitat connectivity in Southeast Asian tropical forests.

Abstract in Malay is available with online material.

*Key words:* auto-gyrating fruit; Borneo; Dipterocarpaceae; tropical forest; seed dispersal; wing-loading

SEED DISPERSAL OCCUPIES A CRITICAL POSITION IN PLANT ECOLOGY. Differential seed dispersal among species influences community structure and dynamics (Rees *et al.* 2001), is a key parameter in neutral (Hubbell 2001) and density dependent (Janzen 1970, Connell 1971) mechanisms of species coexistence, maintains gene-flow between populations, and determines migration rates (Higgins & Richardson 1999, Cain *et al.* 2000). However, quantitative descriptions of seed dispersal are rare; one recent review found only 34 quantitative estimates of seed dispersal from tropical tree species (Kettle 2012). This scarcity of quantitative data is due to the difficulty of measuring dispersal (Bullock *et al.* 2006), which in case of animal dispersed (zoochorous) species includes disperser feeding visits per hour, disperser home range size, gut passage times, and maximum flight range (Howe 1977, Russo *et al.* 2006). Elucidating the full extent of wind-dispersed (anemochorous) species' dispersal potentials is hampered by the difficulty of tracking often many hundreds or thousands of tiny windborne seeds capable of dispersing long-distances, particularly during extreme events such as tropical storms (Nathan *et al.* 2008). Such long-distance dispersal (LDD) events create long, fat-tailed dispersal kernels, for which traditional methods of measuring dispersal (including experimental release, seed traps, and transects) are inadequate (Higgins *et al.* 2003, Nathan 2006, Nathan *et al.* 2008).

Research on anemochorous diaspores has turned to mechanistic modeling to overcome these constraints (Nathan *et al.* 2011). Simple ballistic models have evolved to complex multi-level models incorporating a range of plant traits, fruit morphologies, release

heights, wind speeds, turbulence, and habitat variables (Kuparinen *et al.* 2007, Bohrer *et al.* 2008, Greene & Quesada 2011, Nathan *et al.* 2011, Fontan *et al.* 2013, Damschen *et al.* 2014). Field experiments confirm these mechanistic models are better at estimating long-distance dispersal events than phenomenological models (Soons *et al.* 2004). Despite their complexity, analysis of these models repeatedly confirms that, together with height of release (Thomson *et al.* 2011), the terminal velocity of the seed is the most important variable in predicting dispersal distance by wind (Tamme *et al.* 2014). Seeds with low terminal velocities increase their time span in the air column and hence opportunity to be dispersed horizontally and vertically by turbulence (Green 1980).

The terminal velocity of a falling fruit is proportional to the square root of its “wing-loading,” defined as fruit mass divided by wing surface area (Green 1980, Augspurger 1986). In an analysis of the terminal velocity of diaspores from 34 Neotropical tree species, Augspurger (1986) additionally observed that the slope of the relationship between rate of descent and wing-loading differed significantly between a range of aerodynamic groups, including auto-gyrating, rolling auto-gyrating, undulating, tumbling, and helicopter-like. Despite the importance of terminal velocity, a recent analysis predicting maximum dispersal distances from plant traits included only 53 entries for the terminal velocities of trees with adaptations to wind dispersal (Tamme *et al.* 2014), and Augspurger (1986) paper remains the only published study providing terminal velocities of tropical tree diaspores.

In this paper, we present the first estimates of seed terminal velocities for Paleotropical trees, and expand the dataset for the number of helicopter-like auto-gyrating fruit from 3 to 19, by measuring the terminal velocity of 16 species of Dipterocarpaceae

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on Borneo. Estimates of the terminal velocity as a basis for the subsequent generation of dispersal kernels is of both applied and theoretical importance for Southeast Asian tropical rain forests. Differences in terminal velocity and hence seed dispersal potential between species might play a role in maintaining species coexistence (Hubbell 2001). Critically, lowland tropical forests in the Malesiana region are dominated by dipterocarps which typically account for over 30 percent of basal area in these forests (Newbery *et al.* 1992, Curran & Leighton 2000, Lee *et al.* 2004), and are economically important due to their valuable timber. The extraction of timber coupled with rapid land-use change has left the forests of Southeast Asia largely fragmented and degraded (Sodhi *et al.* 2009, Wilcove *et al.* 2013), and hence an improved understanding of dipterocarp seed dispersal has direct relevance to the regeneration of logged forests and habitat connectivity and associated gene-flow in these Southeast Asian tropical forests (Kettle 2012, McConkey *et al.* 2012).

Dipterocarp fruit have between zero and five elongated sepals which act as wings to disperse the fruit via gravity or gyration (Suzuki & Ashton 1996, Smith *et al.* 2015). We collected mature fruit belonging to 16 dipterocarp species from five genera (one *Dipterocarpus*, one *Dryobalanops*, three *Hopea*, two *Parashorea*, and nine *Shorea*) (Table 1) found in the Sepilok Forest Reserve (SFR) (5°51' N 117°56' E) or the Danum Valley Conservation Area (DVCA), Sabah, Malaysian Borneo. SFR is a 4420 ha fragment of primarily tropical lowland dipterocarp forest, ranging in altitude 0–170 m asl (Fox 1973). DVCA is a 438 km<sup>2</sup> area of uninhabited primary lowland dipterocarp forest (Marsh & Greer 1992). Fruit were collected from the ground during the 2014 community-wide mast fruiting event occurring between July and September.

The fruit fresh mass (g), and lengths and widths of the wings and nut (cm) were measured for each fruit. From these data the wing-loading was calculated, defined as fruit mass divided by “long” wing area. We convert mass to force in millidynes (mg·cm/s<sup>2</sup>) to be consistent with Augspurger (1986); however, millidynes can be converted to an equivalent SI unit nanonewtons (nN) by multiplying by ten. Wing areas were calculated by summing the products of individual wing lengths and widths in the genera *Dipterocarpus*, *Dryobalanops*, and *Hopea*, which possess equal-sized wings. Species in the genus *Parashorea* and *Shorea* have two “short wings” and three “long wings.” Short wings were excluded from the wing-loading calculation as their effect on lift is expected to be limited (Suzuki & Ashton 1996, Smith *et al.* 2015).

Fruits were released from a height of 12.5 m from the balcony of the Sabah Forest Department Research Centre in Sepilok, and at DVCA from an 18 m tree tower. Terminal velocity (m/s) was calculated by dividing the distance fallen by the time taken to hit the ground. Each fruit was released once. Fruits were released individually and, to ensure accuracy of terminal velocity measurements, in the early morning when wind speeds were <1 m/s to limit the effect of turbulence. An electronic anemometer (Windmaster 2, Kaindl Electronic, Germany) mounted at the release height (*i.e.*, 12.5 m in Sepilok and 18 m in Danum) was used to record wind speed (m/s) during fruit release. Following release the fruit were recovered and the wings were removed from a subsample using a scalpel. The wings were subsequently scanned using a flat-bed portable scanner (CanoScan LiDE 110; Canon Inc., Tokyo, Japan) and the mass of the nut without wings was measured. The total wing area of each fruit was calculated from the scans using ImageJ software (Rasband 1997–2014).

TABLE 1. Summary statistics (Means ± SE) relating to fruit morphology, experimentally derived terminal velocity, and predicted dispersal distance using the ballistic model of the 16 dipterocarp study species.

Species	No.	Fruit mass (g)	$\sqrt{\text{wing} - \text{loading}}$ ([mg·cm/s <sup>2</sup> ]/cm <sup>2</sup> )	Terminal velocity (m/s)	Scanned wing area (cm <sup>2</sup> )	Fruit mass excluding sepals (g)	Predicted dispersal distance (m)
<i>Dipterocarpus grandiflorus</i>	17	43.38 (±2.95)	486.6 (±13.96)	4.09 (±0.16)	176.14 (±4.32)	42.80 (±3.23)	23.13
<i>Dryobalanops lanceolata</i>	83	8.91 (±0.21)	371.2 (±5.10)	2.94 (±0.04)	49.78 (±0.82)	6.81 (±0.17)	32.13
<i>Hopea ferruginea</i>	52	0.22 (±0.01)	166.1 (±2.85)	1.36 (±0.05)	5.56 (±0.11)	NA	69.70
<i>Hopea nervosa</i>	57	1.14 (±0.03)	210.5 (±3.67)	1.49 (±0.05)	21.81 (±0.64)	0.77 (±0.04)	63.29
<i>Hopea sp.</i>	45	3.82 (±0.10)	451.5 (±11.71)	3.46 (±0.12)	15.31 (±1.11)	2.95 (±0.15)	27.28
<i>Parashorea malaanonan</i>	40	5.51 (±0.19)	297.5 (±5.58)	2.08 (±0.08)	59.60 (±2.35)	4.11 (±0.14)	45.40
<i>Parashorea tomentella</i>	140	8.32 (±0.16)	317.0 (±7.63)	2.12 (±0.05)	67.93 (±2.67)	6.48 (±0.18)	44.52
<i>Shorea argentifolia</i>	31	0.80 (±0.03)	168.8 (±3.86)	1.22 (±0.07)	23.59 (±0.62)	NA	77.38
<i>Shorea beccariana</i>	41	9.43 (±0.25)	327.0 (±3.52)	2.20 (±0.07)	80.90 (±2.10)	5.34 (±0.29)	42.91
<i>Shorea johorensis</i>	36	2.65 (±0.08)	225.0 (±2.26)	1.66 (±0.06)	50.74 (±1.13)	1.80 (±0.08)	56.83
<i>Shorea leprosula</i>	138	1.06 (±0.02)	208.7 (±2.21)	1.62 (±0.03)	19.25 (±0.43)	0.65 (±0.02)	58.42
<i>Shorea macrophylla</i>	42	34.50 (±1.26)	516.0 (±13.62)	4.04 (±0.15)	129.65 (±7.31)	NA	23.41
<i>Shorea mexistopteryx</i>	37	15.30 (±0.39)	342.3 (±5.57)	2.38 (±0.08)	127.61 (±2.56)	8.69 (±0.35)	39.75
<i>Shorea parvifolia</i>	70	0.95 (±0.03)	175.0 (±2.58)	1.36 (±0.05)	27.46 (±0.92)	NA	69.61
<i>Shorea seminis</i>	48	2.63 (±0.14)	621.9 (±18.99)	5.39 (±0.16)	9.38 (±0.35)	2.83 (±0.17)	17.54
<i>Shorea smithiana</i>	75	6.33 (±0.13)	298.8 (±4.41)	1.90 (±0.06)	77.82 (±1.93)	2.98 (±0.14)	49.77

Mean  $\sqrt{\text{wing-loading}}$  ( $[\text{mg}\cdot\text{cm}/\text{s}^2]/\text{cm}^2$ ) ranged from 166.1 in *H. ferruginea* to 621.9 in *S. seminis* (Table 1). A linear regression between terminal velocity and  $\sqrt{\text{wing-loading}}$  showed a highly-significant positive relationship ( $R^2 = 0.97$ ;  $F_{1,14} = 429.3$ ;  $P < 0.001$ ) (Fig. 1), confirming that dipterocarp species with lower ratios of fruit mass to wing area descend over a longer period of time. The high R-squared value ( $R^2 = 0.97$ ) confirms this relationship is consistent across the family and fruit morphologies given that the 16 data points represent species in five genera. To assess if the model was sensitive to data from individual species, we reran the regression 100 times, using a random selection of 14 of the 16 species in each model. The coefficients were highly consistent between the full species model and models excluding two species at a time (Full model: slope =  $-0.362$ , intercept =  $0.0087$ ; 14 species models: mean slope =  $-0.374$  [95% percentiles:  $-0.466$  to  $-0.226$ ], intercept =  $0.0087$  [95% percentiles:  $0.0082$ – $0.0089$ ]). Despite overlaps in the species composition between Danum and Sepilok, local differences in the species participating in the mast fruiting and timing of fruit abscission meant only *S. leprosula* fruit were released at both locations and release heights. An analysis of variance confirmed that

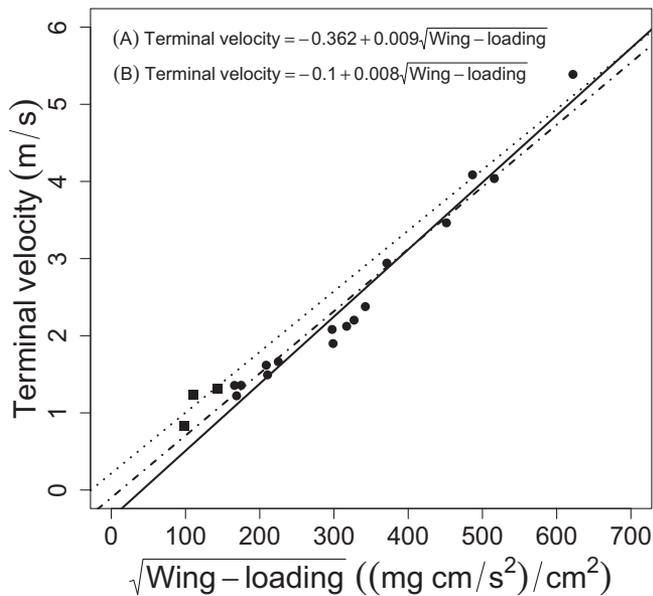


FIGURE 1. Figure one plots mean fruit  $\sqrt{\text{wing-loading}}$  ( $[\text{mg}\cdot\text{cm}/\text{s}^2]/\text{cm}^2$ ) against terminal velocity (m/s) for the 16 dipterocarp species used in this study (circles) and the three 'helicopter-like' species (squares) from Augspurger (1986). The solid line represents the line of best fit from regression of mean fruit  $\sqrt{\text{wing-loading}}$  against terminal velocity for the 16 dipterocarp species, and the regression fitted equation is given by equation A. The dotted line represents the line of best fit for the regression of mean fruit  $\sqrt{\text{wing-loading}}$  against terminal velocity for 'helicopter-like' diaspores from Augspurger (1986). The 'dot-dash' line represents the line of best fit for the regression of mean fruit  $\sqrt{\text{wing-loading}}$  against terminal velocity using the combined dataset of the dipterocarp fruit presented and the three 'helicopter-like' fruit from Augspurger (1986); the regression fitted equation is given by equation B.

there was no significant difference in the terminal velocity of *S. leprosula* fruit released from the two heights ( $F_{1,136} = 0.706$ ;  $P = 0.402$ ) (Fig. S1).

Using the terminal velocities observed, we predicted dispersal distances for each species using the ballistic model presented in (Augspurger 1986), where distance dispersed is calculated as height of release divided by terminal velocity multiplied by wind speed. A release height of 45 m was used, corresponding to the mean canopy height at Sepilok, together with a wind speed of 2.1 m/s (the mean annual wind speed 2000–2014 at Sandakan Airport 11 km from Sepilok) (Tutiempo.net 2015). The mean predicted dispersal distance was 46.32 m, and predictions ranged from 17.5 m in *S. seminis* to 77.4 m in *S. argentifolia* (Table 1). Predictions from the ballistic model must however be interpreted with caution as multiple factors might decrease (e.g., low wind speeds under the canopy [Whitmore 2006], entanglement of fruit in vegetation), or increase these estimates (e.g., timing of fruit abscission [Maurer *et al.* 2013], extreme weather events [Nathan *et al.* 2008], and updrafts [Tackenberg 2003]).

Measurements of total wing area and nut mass are only available for a small subset of dipterocarps, whereas wing dimensions and nut dimensions, from which area and volume can be calculated respectively, are available for almost the complete dipterocarp flora in the Malesiana region (Ashton 1983). We regressed total scanned fruit wing areas against caliper measured wing areas. We also regressed fruit mass against nut volume calculated from nut dimensions. In both cases the relationships between fruit morphology and easily measured proxies was extremely strong (Wing area regression:  $R^2 = 0.99$ ,  $F_{1,15} = 3749$ ,  $P < 0.001$ ; Fruit mass regression:  $R^2 = 0.93$ ,  $F_{1,11} = 131.1$ ,  $P < 0.001$ ) (Figs S2 and S3). Using this approach we calculated the wing loading for 367 dipterocarp species with fruit dimension data contained in the Flora Malesiana (Ashton 1983) (data are presented as minimum and maximum for each dimension and therefore we used mean values to calculate species wing loadings). Terminal velocities for all 367 species were subsequently calculated using the fitted values from the regression model of terminal velocity and wing loading from our 16 species (Fig. 1). These data are presented in the Table S1.

The estimated dipterocarp terminal velocities open up a range of research avenues. Interspecific differences in seed dispersal is a component of multiple species coexistence mechanisms (Janzen 1970, Connell 1971, Tilman 1994, Hubbell 2001). The data can be used to parametrize coexistence models, thereby improving our understanding of this trait in maintaining species richness in hyper-diverse tropical forests. The data also possess applied value. Particularly pertinent, given the rapid pace of deforestation and forest fragmentation, is that of processes of forest regeneration. Logged forests, often surrounded by oil-palm agriculture, are now widespread across Southeast Asia (Koh & Wilcove 2008). Their trajectories of recovery will be shaped by patterns of seed dispersal, establishment, and growth. Opportunities for regeneration are constrained by the low densities of remaining mature trees (Cannon *et al.* 1994, Berry *et al.* 2010, Bagchi *et al.* 2011), which is exacerbated by the limited seed dis-

persal capacities of many dipterocarps (Smith *et al.* 2015). Differential dispersal among species might favor species with longer range dispersal capacities (coupled with regeneration strategy), as such species might be better placed to occupy sites in degraded forests far from competitors. This implies possible shifts in dipterocarp species composition as forest recovery proceeds (Bagchi *et al.* 2011). Should fruit morphologies be linked to other plant traits, such as growth rates and wood density (King *et al.* 2005, 2006, Wright *et al.* 2010), such compositional shifts might have far reaching implications for ecosystem function.

Recent studies suggest that dipterocarp seedlings struggle to recruit naturally in forest fragments under 100 ha in size, though the causes remain unclear (Yeong 2015). This observation casts the long-term persistence of dipterocarps in small fragments into uncertainty as they lack a seed bank, due to the recalcitrant nature of their fruit (Li & Pritchard 2009), and the means to rapidly proliferate as they mast fruit on a supra-annual periodicity (Ashton 1988, Sakai 2002, Brearley *et al.* 2007). Their long-term population persistence might therefore depend on seed influx from larger fragments or contiguous forests and the formation of more resistant meta-populations. Terminal velocities are a necessary prerequisite for accurate models of LDD in wind-dispersed seed and consequently spatial models predicting seed movement between fragments (Soons *et al.* 2005). Our estimates of dipterocarp terminal velocities should catalyze such modeling efforts and generate data necessary for policy-makers to deliver evidence-based management and conservation plans addressing the issue of forest fragment persistence in Southeast Asian agricultural landscape matrices (McConkey *et al.* 2012). We emphasize that such research is timely given the high level of threat faced by the Dipterocarpaceae (Maycock *et al.* 2012) and the additional burden of determining rates of population spread driven by climate change (Higgins & Richardson 1999, Colwell *et al.* 2008, Corlett 2009).

Beyond the Dipterocarpaceae, this study substantially increases the wing loading and terminal velocity data available on helicopter-like fruit from three species to 19. There is no significant difference between the fitted equation of Augspurger's (Augspurger 1986) Neotropical data for helicopter-like fruit and our Paleotropical data (Fig. 1), although the  $\sqrt{\text{wing} - \text{loading}}$  values of Dipterocarpaceae fruit (Table 1) are substantially higher than the measured Neotropical species, which range only between 97.7 and 143.7 ( $[\text{mg}\cdot\text{cm}/\text{s}^2]/\text{cm}^2$ ). We therefore combined the datasets and re-analyzed the wing loading to terminal velocity relationship (Fig. 1), providing an updated regression equation with which to calculate the terminal velocity of helicopter-like diaspores ( $R^2 = 0.95$ ;  $F_{1,17} = 373.4$ ;  $P < 0.001$ ). Recognizing that this equation is derived primarily from data from a single family, the Dipterocarpaceae, we believe it can nevertheless be generalized for helicopter-like diaspores globally with  $\sqrt{\text{wing} - \text{loading}}$  values between 97.7 and 621.9 ( $[\text{mg}\cdot\text{cm}/\text{s}^2]/\text{cm}^2$ ).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. Predicted wing areas, fruit masses,  $\sqrt{\text{wing} - \text{loadings}}$  ( $[\text{mg}\cdot\text{cm}/\text{s}^2]/\text{cm}^2$ ), and terminal velocities with upper and lower CIs for 367 species of Dipterocarpaceae from the Flora Malesiana.

FIGURE S1. Boxplot of the terminal velocity of *S. leprosula* fruit released at Sepilok and Danum.

FIGURE S2. Regression of mean caliper measured long-wing area against scanned total wing area for the 16 dipterocarp study species experimentally released.

FIGURE S3. Regression of mean  $\log(\text{fruit volume}(\text{cm}^3))$  against  $\log(\text{fruit mass}(\text{g}))$  for 12 of the dipterocarp study species experimentally released.

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