Seed dispersal by wind in Kirindy Forest: relationships between wing loading, seed shadows and tree heights

Froukje Postma, Groningen University, the Netherlands

Rence Randrianindrina, University of Antananarivo, Madagascar

Sendi Baptista, Catholic University of Angola, Angola

Abstract

The objective of this study was to investigate how the traits of wind dispersed propagules relate to dispersal distance within a species (intraspecific) and between different species (interspecific). Between species, we hypothesised that tree species face a trade-off between canopy height and wing loading, mass per surface area of the seed. We measured seed shadows and seed traits of six wind dispersed tree species. We found that time of descent (TOD) was negatively related to wing loading, intra and interspecific. Within a seed shadow, there were no differences in wing loading and TOD. However, wing loading seems to affect the shape of the seed shadow of a tree species. We didn't find evidence for an interspecific trade-off between wing loading and tree height, although there is a tendency.

INTRODUCTION

Seed dispersal is one of the most critical stages in the life history of plants. It is an important process because it can reduce the risk of predation and parasitism as it gives seeds the possibility to 'escape' from affected conspecifics (Howe & Smallwood, 1982). Besides this, dispersal diminishes potential interspecific competition. Several studies have shown that seeds with a larger dispersal distance have a larger survival chance of establishment (Bawa & Hadley, 1990).

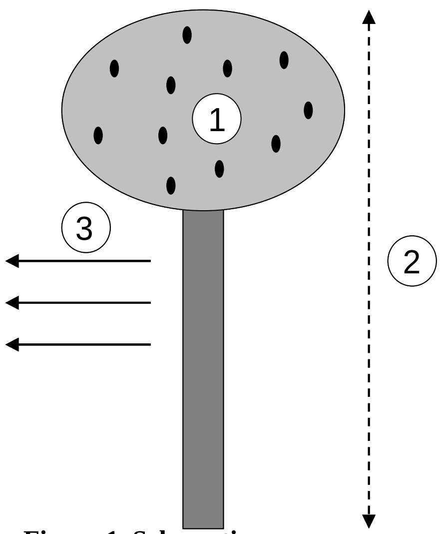


Figure 1. Schematic representation of features needed for wind dispersal.

There are three main mechanisms by which the fruits and seeds of plants can be dispersed: by animals, by water and by wind. The dispersal distances for seeds dispersed by animals depend on the gut passage rate and on the animal movements. The longer a seed remains in the gut of the animal and the larger the displacement of the animal, the further away a seed will be dispersed.

Dispersal by wind is determined by other factors: (1) seed traits affecting the time of descent (TOD), (2) the canopy height of the tree and (3) the wind speed at moment of dispersal (Figure 1).

The most important seed trait determining dispersal success by wind is wing loading. Wing loading describes the ability of wings to lift mass, which is calculated as the mass per surface area of the wings. The same principle can be applied to seeds to describe their ability to disperse. Seeds or fruits with a low mass compared to the surface area of the propagule will have a low wing loading and will consequently take longer time to reach the ground, increasing their potential dispersal distance by the wind. Besides wing loading, the shape of the seed may also influence the TOD and/or effectiveness of the wind.

Although many plant species depend on wind for the dispersal of their seeds, not much is known about the mechanisms and traits of wind dispersal compared to animal dispersal. Therefore, the objective of this study is to investigate how the traits of wind dispersed propagules relate to dispersal distance within a species (intraspecific) and between different species (interspecific).

Seeds from the same tree are distributed at different distances from the tree canopy. This raises the question how important the role of seed traits, like wing loading, is in determining dispersal distance within a species:

1. Is there an intraspecific relation between wing loading and TOD?
2. Do seeds with a longer dispersal distance have a lower wing loading?

Seeds with larger wings will be more successful dispersers. However, wings consist of biomass and are thus an investment for the plant. Production of large wings means that this biomass cannot be allocated to other plant functions, e.g. the canopy or seed production itself. But not only seed traits determine the dispersal success of a plant species. The average canopy height of a species is expected to play an important role as well, as the TOD of the seed does not only depend on the seed traits, but also on the height from which it drops. Therefore, we expect that tree species face a trade-off between canopy height and wing loading, where large tree species can ‘afford’ a higher wing loading to disperse its seeds as far as a small tree. To test this hypothesis, we asked the following questions:

3. Is there an interspecific relation between average TOD and average wing loading?
4. Is there an interspecific relation between tree height and average TOD, and between tree height and wing loading?
5. Is there an interspecific relationship between seed shadow and TOD?

METHODS

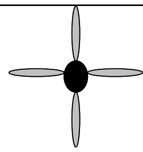
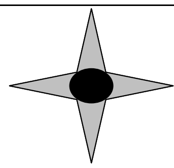
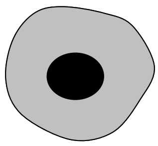
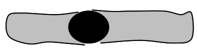
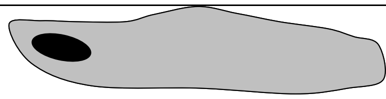
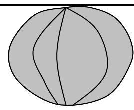
Study site

The study was carried out in Kirindy forest, 60 km northeast of Morondava and 20 km inland from the west coast of Madagascar between 14 – 20 November 2010. This forest is situated between 20º01’ - 20º04’S and 44º32’ - 44º44’E (Besairies, 1973) with an elevation around 40 m above the sea level. It is a dry deciduous forest growing on sandy soils and covers about 10,000 ha (Besairies, 1973). The site is characterised by a short rainy season (December-March) with an annual rainfall averages between 700 mm to 800 mm (Garbutt, 1999). The mean temperature is 25.1 ºC and the mean speed of wind in this region is 2.4 m/sec (Raivoarisoa, 1999).

Study species

Six wind dispersed species were selected for this study. Table 1 shows some characteristics of the species studied.

Table 1. Description of plant species studied

Plants species	Family	Life form	Dispersing agent	Schematic representation of the fruit/seed
Foetidia asymetrica	LECYTHIDACEAE	Deciduous tree	Fruit	
Foetidia retusa	LECYTHIDACEAE	Deciduous tree	Fruit	
Neobeguea mahafaliensis	MELIACEAE	Deciduous tree	Seed	
Stereospermum euphoroides	BIGNONIACEAE	Deciduous tree	Seed	
Hildegardia erythrosiphon	MALVACEAE	Deciduous tree	Seed	
Combretum coccineum.	COMBRETACEAE	Liana	Seed	

Seed shadows

We measured seed shadows, the distribution of seeds around the tree, for the species *F. asymetrica*, *N. mahafaliensis* and *S. euphoroides*. For those measurements, we selected individuals without conspecifics within a radius of 10 m. Around each tree, four transects were laid in North, South, West and East directions, and in each transect three plots were placed, representing different distance classes from the tree canopy (Figure 2):

- (1) distance class 1: next to tree trunk; under tree canopy
- (2) distance class 2: just outside the edge of the canopy
- (3) distance class 3: 3 m out of the canopy

The plot sizes were 0.25 m^2 for *F. asymetrica* and *S. euphoroides*, and 1.0 m^2 for *N. mahafaliensis*. In each plot, we counted and collected all seeds. For *N. mahafaliensis*, some seeds were affected by predispersal parasitism. As this clearly had an effect on the dispersal ability of the seeds, only the non-parasitised seeds were used. In total, we measured the seed shadows of four *F. asymetrica* trees, five *N. mahafaliensis* trees and five *S. euphoroides* trees.

Seed traits

For *N. mahafaliensis* and *F. asymetrica*, 24 seeds from distance class 1 and 24 seeds from distance class 3 were randomly selected from the tree individuals used on the seed shadows. We did not use

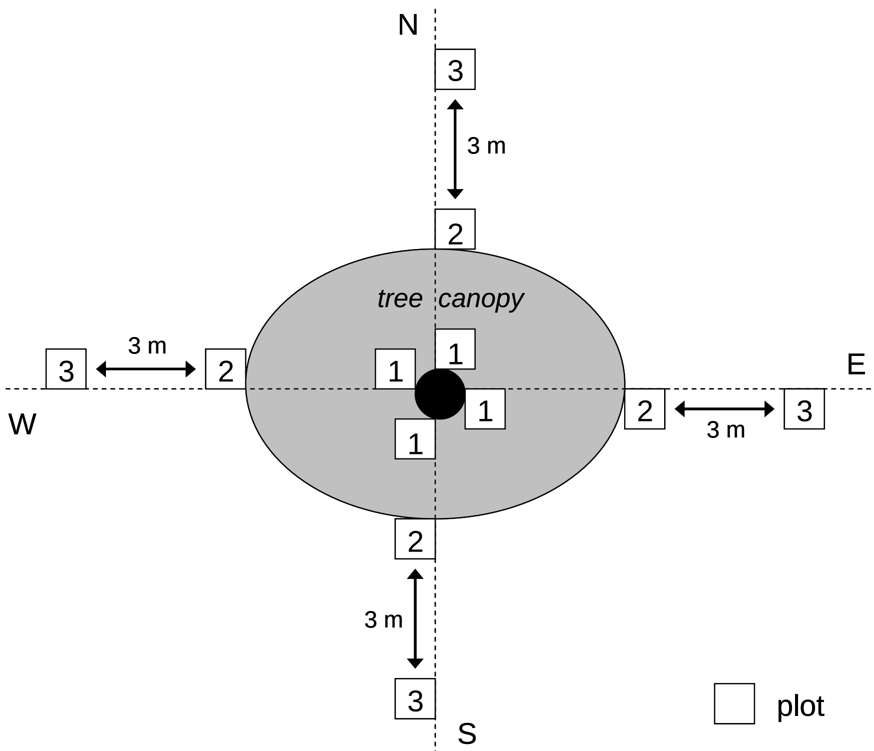


Figure 2. Seed shadow sampling of the trees. The transects were placed in four directions. Three plots per transect were placed in different distance classes from the canopy.

the seeds of the different distance classes for *S. euphoroides* because the majority of the seeds was already damaged when collected in the field.

For *F. retusa*, *S. euphoroides* and *C. coccineum*, 24 seeds were collected in the field from four different tree individuals each. For *H. erythrosiphon*, 22 seeds from one tree were used. For each seed, we measured:

- Mass - with an electronic balance.
- Surface area - with a scanner with high resolution using the “LeafArea” software from Plant Ecology Unit at the University of Sheffield in the UK. Translucent propagules were painted with black ink before scanning.
- Time of descent (TOD) from 6.3 m height. TOD was measured with stopwatches by three different persons, and the mean time was used for further analysis.

Tree height was measured with a clinometer for all tree individuals used in the field.

Data analysis

Wing loading was defined as mass per surface area of the seeds. TOD and wing loading were compared for the distance classes 1 and 3 with a one-tailed t-test, predicting that distance class 1 > distance class 3. The intraspecific relationships between TOD and wing loading were tested for all six species with linear regression. The interspecific relationships between TOD and wing loading, TOD and tree heights, and wing loading and tree heights were tested with linear regression. All data analyses were performed in EXCEL 2003.

RESULTS

Intraspecific relationship wing loading and TOD

Figure 3 shows a negative relationship between wing loading and TOD for the seeds of *F. asymetrica* ($R^2 = 0.496$, $p < 0.001$), *F. retusa* ($R^2 = 0.235$, $p = 0.016$), *N. mahafaliensis* ($R^2 = 0.498$, $p < 0.001$) and *C. coccineum* ($R^2 = 0.231$, $p = 0.017$). We found no relation between wing loading and TOD for the seeds of *H. erythrosiphon* ($R^2 = 0.022$, $p = 0.512$) and *S. euphoroides* ($R^2 = 0.052$, $p = 0.284$).

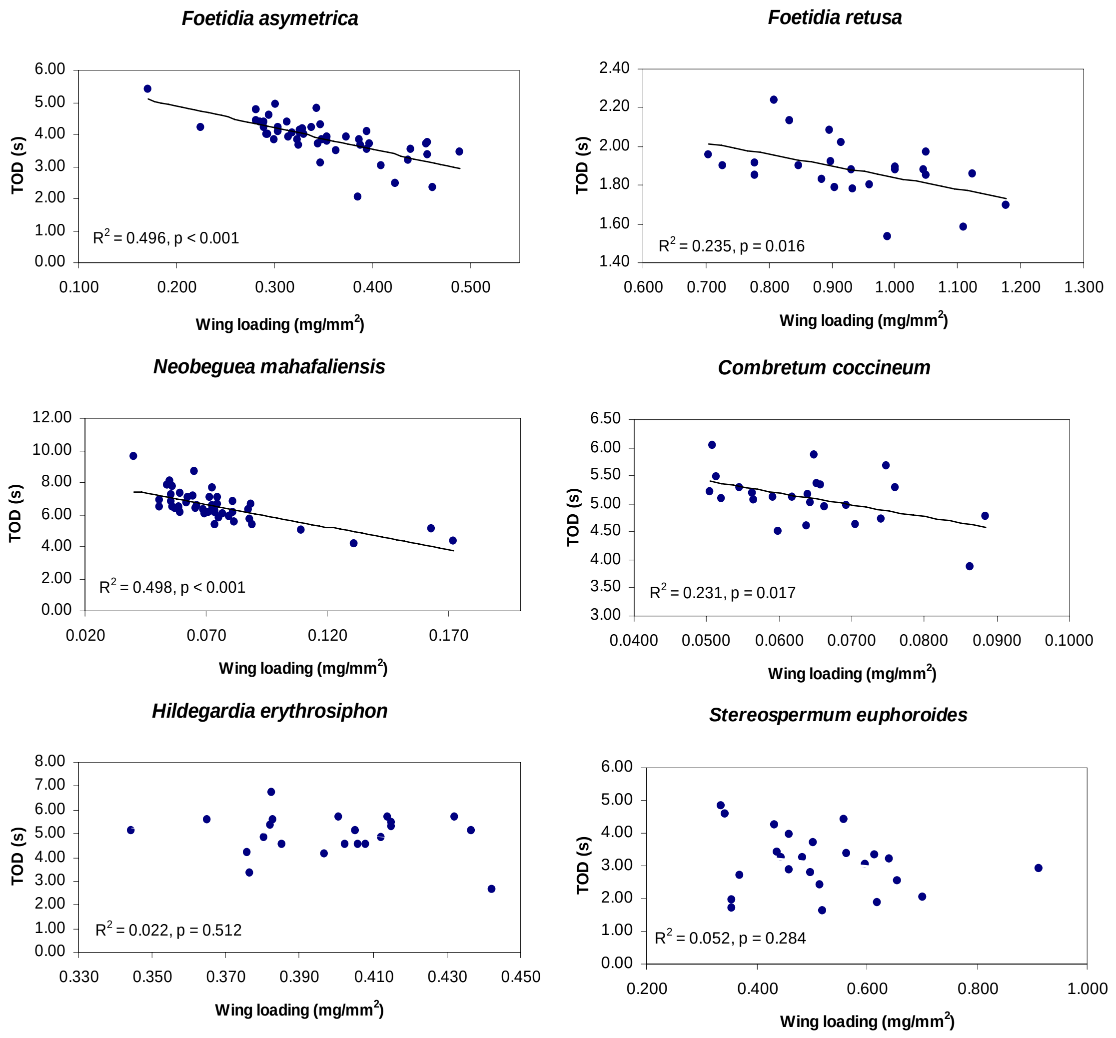


Figure 3. The relationship between TOD (seconds) and wing loading (mg/mm^2) for the six different tree species. R^2 and p-value (*p*) is shown for each species. Each data point represents a single seed.

Intraspecific relationship dispersal distance and wing loading

For *F. asymetrica*, we found no significant differences in TOD ($t = 1.679$, $p = 0.336$) and wing loading ($t = 1.679$, $p = 0.239$) between the seeds from distance class 1 and distance class 3. For the species *N. mahafaliensis*, there were no differences in seed traits between the two distance classes 1 and 3 (TOD: $t = 1.680$, $p = 0.428$; wing loading: $t = 1.680$, $p = 0.100$).

Interspecific relationship TOD and wing loading

There was a significant negative relationship between the mean TOD and the mean wing loading per tree species (Figure 4, $R^2 = 0.832$, $p = 0.011$).

Interspecific relationship tree height and TOD/wing loading

Figure 5 shows that there is no significant relationship between mean TOD and mean tree height, although there seems to be a negative trend (R^2 = 0.681, p = 0.085). As represented in Figure 6 the mean wing loading has no significant relationship with mean tree height per species (R^2 = 0.546, p =0.154).

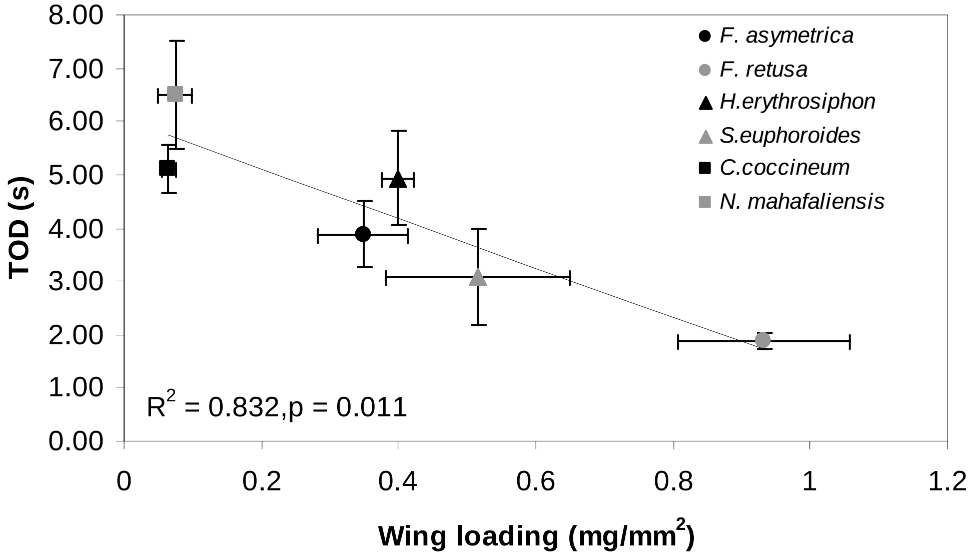


Figure 4. **The relationship between mean TOD (seconds) and mean wing loading (mg/mm^2) for the six different tree species. The bars represent standard deviation. R^2 and p-value (*p*) are shown.**

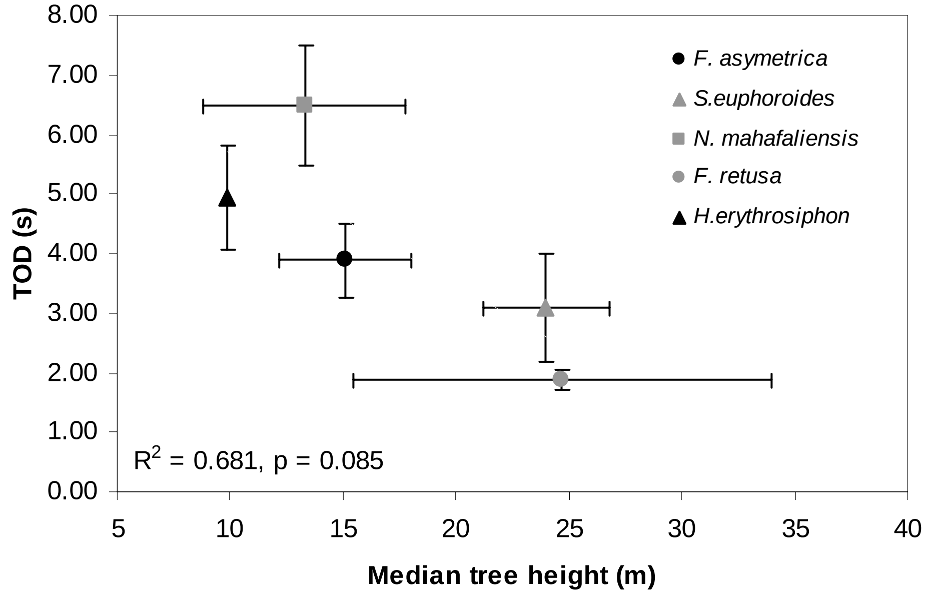


Figure 5. The relationship between mean TOD (seconds) and mean tree height (meters) for the six different tree species. The error bars represent standard deviation. R^2 and p-value (*p*) are shown.

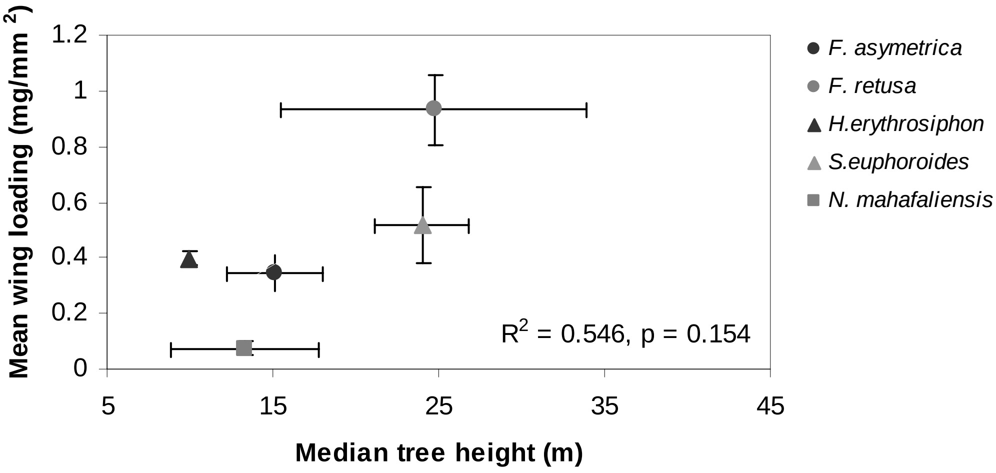


Figure 6. The relationship between mean wing loading (mg/mm^2) and mean tree height (meters) for the six different tree species. The error bars represent standard deviation. R^2 and p-value (*p*) are shown.

Interspecific relationship seed shadow and TOD

Figure 7 shows the seed shadows of the three species *F. asymetrica*, *N. mahafaliensis* and *S. euphoroides* as the mean percentage of seeds per distance class. *F. asymetrica* and *S. euphoroides* have a similar seed shadow, with a decreasing number of seeds with increasing distance from the tree trunk. The seed shadow of *N. mahafaliensis* is different; the number of seeds increases from the edge of the canopy to 3 meters outside the edge. As Figure 4 and 5 show, the TOD of *F. asymetrica* and *S. euphoroides*is are not significantly different: the TOD of seeds of *F. asymetrica* is 3.89 ± 0.62s (mean ± SD) and the TOD of the *S. euphoroides* 3.09 ± 0.91s (mean ± SD). *N. mahafaliensis* has a larger TOD of 6.49 ± 1.00s (mean ± SD).

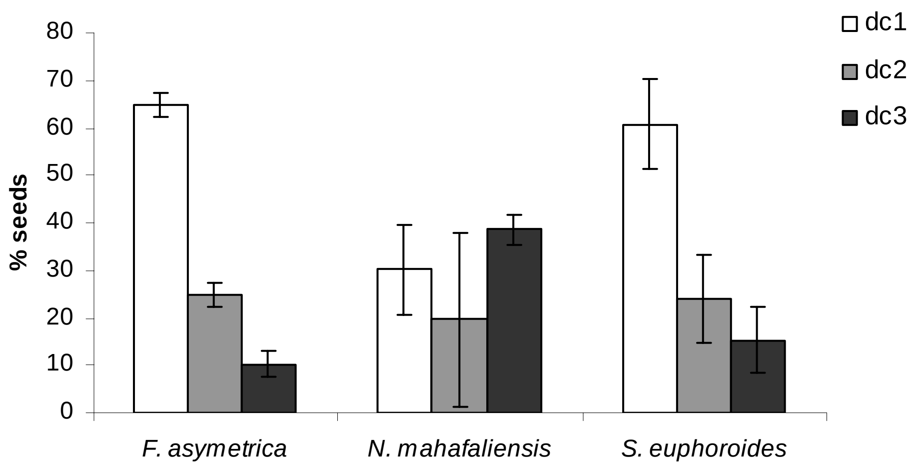


Figure 7. Mean percentage of seeds (%) per distance class (dc) for the three species sampled in the seed shadows. The error bars represent standard deviation.

DISCUSSION

The objective of our study was to investigate how the traits of wind dispersed propagules relate to dispersal distance within a species (intraspecific) and between different species (interspecific). We found that time of descent (TOD) was negatively related to wing loading, both within species as between species. Within a seed shadow, there were no differences in wing loading and TOD between seeds with a large or a small dispersal distance. But wing loading does seem to affect the shape of the seed shadow of a tree species. We didn't find evidence for an interspecific trade-off between wing loading and tree height.

Intraspecific relationship wing loading and TOD

For four of the six species tested, we found a negative relation between the TOD and wing loading. This was expected, as seeds with a low wing loading have a low mass per surface area and subsequently a higher TOD. The amount of variation in TOD explained by wing loading ranged from ~20 to ~50 %. This indicates that wing loading plays an important role in determining TOD, but that other factors affect it as well, possibly the (a)symmetry of the seeds. Besides this, the height used for measuring TOD (6.3 m) has likely added extra variation in the TOD independent of the seed traits itself; in the first meter of descent some seeds dropped clearly faster due to their position at moment of release.

The absence of a relation between wing loading and TOD in *H. erythrosiphon* might be due to the small range in wing loading. The species with a significant relationship had a 2 – 5 fold range in wing loading while the range of *H. erythrosiphon* differs only 1.3 fold. Also for *S. euphoroides*is we didn't find a significant relationship. The determination of the surface area of the seeds was not as accurate as for the other species, because the wings were too fragile to paint and scan precisely.

Intraspecific relationship dispersal distance and wing loading

The absence of a relationship between dispersal distance and wing loading within a seed shadow might be due to the fact that our distance classes were not far enough from the tree to detect differences in wing loading. Our maximal distance class was 3 m out of the canopy, which is likely to be very small compared to the end of the actual seed shadow. An extra factor determining dispersal distance is the wind speed at the moment of propagule detachment. Wind speed is very irregular, and can thus easily cause different dispersal distances for seeds with the same wind dispersal traits.

Interspecific relationship TOD and wing loading

We found a strong significant relation between mean TOD and wing loading. Even for only 6 species, more than 80% of the variation in TOD was explained by wing loading. This indicates that wing loading is by far the most important factor determining TOD, and thus dispersal distance, and that other factors like shape and symmetry have only a minor effect.

Interspecific relationship tree height and wing loading / TOD

We hypothesised that there would be a trade-off for tree species between tree height and wing loading: tall species can 'afford' a higher wing loading. However, we didn't find a significant relation between wing loading and tree height. Nevertheless, the relation between TOD and tree height was almost significant (0.085). This could be a good indication that a trade-off might exist, especially taking into account the sample size (N=4). Besides this, tree height was measured for only a small number of individuals, which might not represent the average height of a species.

Interspecific relationship seed shadow and TOD

Although it was not statistically tested, it seems that TOD determines the shape of the seed shadow of a tree. The error bars are high, but that is likely an artefact of the plot sizes and sample sizes. The TOD has probably even more large-scale effects, like species distribution. In the field, we noticed that *F. asymetrica* and *F. retusa* individuals were often standing close together, which can be the results of the high TOD of these species propagules. In contrast, *N. mahafaliensis* individuals were always isolated, which is in line with the low wing loading and the shape of the seed shadow of this species.

CONCLUSION AND RECOMMENDATIONS

As shown, wing loading is a very important seed trait, determining TOD and dispersal distance from a tree both in intra and interspecific comparisons. For future works, it would be interesting to investigate if the interspecific relationship holds if more wind dispersed species with even more seed shapes are added. Another study approach would be to investigate the relation between seed shadows of species, species distributions and small scale community diversity.

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