

Wind-Generated Seed Shadow in Southern Brazil: The Influence of the Mother Plant and Wind Direction

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Abstract

Diaspore dispersal is an essential function of plant species, with effects on plant populations and natural forest dynamics. This study examines how traits of the mother plant (height, crown spread and distance from the diaspores) and the wind (wind speed) affect the spatial distribution of anemochorous diaspores of *Apuleia leiocarpa*, *Peltophorum dubium*, and *Jacaranda micrantha* in Southern Brazil. The number of diaspores from *A. leiocarpa*, *P. dubium*, and *J. micrantha* decrease with the increase in distance from the mother plant and there was no influence of wind direction on the spatial distribution of diaspores. Diaspore sizes of these plants were not related to their dispersal distances. Diaspore dispersal for *A. leiocarpa* was negatively correlated to the plant height and the crown spread. The dispersal of *Peltophorum dubium* and *Jacaranda micrantha* were not influenced by the diaspores and plants traits considered in this study.

Keywords: Brazilian Atlantic Forest, biodiversity conservation, dispersal syndrome, spatial distribution of diaspores.

1. INTRODUCTION AND OBJECTIVES

Dispersal is a critical ecological process with consequences for plant reproduction, population and community dynamics, and gene flow among populations (Croteau, 2010; Robledo-Arnuncio et al., 2014). Knowledge of dispersal strategies has long been recognized as important for understanding plant evolution processes, as well as for explaining current distribution of plants across landscapes (Kuhlmann & Ribeiro, 2016; Sadló et al., 2018). Nowadays, such knowledge has become essential to understand, predict and manage the responses of individuals, populations and species to ecosystem perturbation and climate changes (Robledo-Arnuncio et al., 2014).

The dispersal units of plants, called diaspores, comprise fruits, seeds or other plant particles (Van der Pijl, 1982) moved away from the individual in which they were born to another location where they will settle and reproduce (Croteau, 2010). Diaspores can be dispersed by several agents, including biotic (animal or self-dispersal) and abiotic ones (such as wind or water) (Martins et al., 2014). Anemochorous species exhibit diaspores of small size and mass that are light enough for dispersal by wind (Van der Pijl, 1982). Such diaspores are classified as flyers (balloon, winged, plumed and dust

diaspores), rollers or throwers (Van der Pijl, 1982). They can alternatively be classified according to their morphological and aerodynamic traits in still air as floater, autogyro, rolling autogyro, undulator or helicopter (Augsburger, 1986).

In addition to diaspores morphological and aerodynamic traits, factors such as wind conditions, height of the mother plant and characteristics of the surrounding vegetation influence the mean potential dispersal distance of anemochorous diaspores, which may be carried over long distances or be concentrated under the canopy of the mother plant (Horn et al., 2001; Thomson et al., 2011). The spatial distribution resulting from the diaspore dispersal around the mother plant (source) is known as “seed shadow” (Nathan & Muller-Landau, 2000). Studies about seed shadows on local and larger spatial scales enable the identification of differences in the seed dispersal of species, and consequently provide insights into the processes, which structure plant communities (Clark et al., 2005).

Many studies have shown that dispersal distances are strongly related to the seed dispersal mode (Arjona et al., 2018; Seidler & Plotkin, 2006). Other studies have demonstrated that there is wide variation in dispersal distances among species that share the same seed dispersal mode (Clark et al., 2005; Muller-Landau et al., 2008). Researchers have recently been studying

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the influence of plant traits (such as growth form, height and others) on dispersal distances and seed shadow (Augspurger et al., 2017; Tamme et al., 2014; Thomson et al., 2011). For Neotropical species, Augspurger et al. (2017) showed that wind dispersal is predicted more accurately by the plant height rather than by diaspore traits. These studies are scarce for tropical species from the Atlantic Forest, especially when anemochorous species and seasonal forests are considered.

While the effects of forest fragmentation (Herrera & García, 2010) and animal extinctions (Pires et al., 2018) on animal-dispersed plants are well studied, the effects of such factors on wind-dispersed species remain unknown. Because wind-dispersed species seem to benefit from open environments (Silva et al., 2017), they are especially important for colonizing areas after natural or anthropogenic disturbances (Martini & Santos, 2007). In Europe, Montoya et al. (2008) observed that wind-dispersed species are more vulnerable to forest fragmentation than animal-dispersed species. In Brazil, studies about seed shadow of anemochorous species are scarce and the ones about the effects of Atlantic Forest fragmentation on the seed shadow of anemochorous species are nonexistent. Thus, improved understanding regarding the seed shadow of these species, as well as how the diaspores and plant traits influence them, is important for devising management strategies for these species and predicting the potential for recovery of such areas following natural (such as forest gaps) or anthropogenic disturbances.

Therefore, this study conducted a field experiment to evaluate the spatial distribution of anemochorous diaspores of *Apuleia leiocarpa* (Vogel) J.F. Macbr., *Peltophorum dubium* (Spreng.) Taub. and *Jacaranda micrantha* Cham. and their relationship with the distance from the mother plant, height and crown spread of trees and wind speed. Three emergent species were chosen to avoid the influence of plant growth

form on the spatial distribution of the seeds. All studied species commonly occur in the emergent layer of the Seasonal Deciduous Forest and produce rolling autogyro diaspores. However, *A. leiocarpa* and *P. dubium* diaspores are fruits, while *J. micrantha* diaspores are seeds. In addition to being larger, *P. dubium* and *A. leiocarpa* diaspores are heavier than those of *J. micrantha*, as reported in literature (Lorenzi, 1992). Therefore, a larger percentage of *J. micrantha* diaspores should be expected compared with *A. leiocarpa* and *P. dubium* in areas distant from the mother plant. Specifically, the following questions are addressed: 1) Does the diaspore density of *A. leiocarpa*, *P. dubium*, and *J. micrantha* decrease with an increase in distance from the mother plant? 2) Does the dispersal distance of *A. leiocarpa*, *P. dubium*, and *J. micrantha* diaspores increase with an increase in tree height and crown spread? 3) Are the spatial distributions of *A. leiocarpa*, *P. dubium*, and *J. micrantha* diaspores influenced by wind direction?

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in the National Forest of Chapecó (Figure 1), in the western region of the state of Santa Catarina, southern Brazil (27° 5' 19.9" S latitude and 52° 46' 47.3" W longitude) (ICMBio, 2013). The National Forest of Chapecó covers 1,590.60 ha and is divided into three zones (called "glebas"): Gleba I (1,287.54 ha), Gleba II (302.62 ha) and Gleba III (0.433 ha) (ICMBio, 2013). This study was carried out in Gleba I. The natural vegetation in the National Forest of Chapecó comprises Mixed Ombrophilous Forest and Seasonal Deciduous Forest (ICMBio, 2013), with the latter characterized by the loss of the emergent tree foliage during autumn and winter (IBGE, 2012).

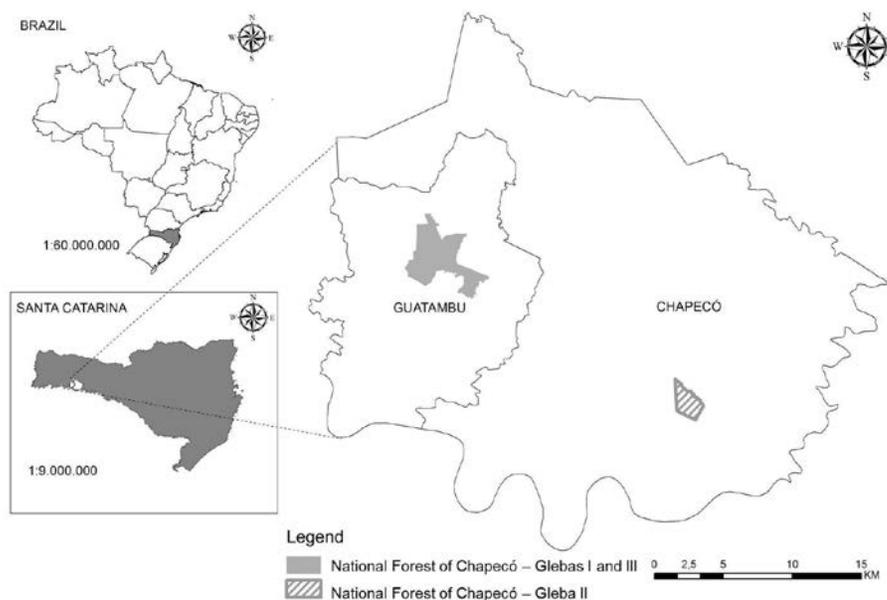


Figure 1. Localization of the National Forest of Chapecó, Santa Catarina State, Southern Brazil.

The climate in the region is Cfa according to the Köppen classification, i.e., a mesothermal humid subtropical climate with hot summers, rains distributed throughout the year, and severe frost (Köppen, 1948). Data on monthly rainfall (mm), maximum wind speed (km/h) and wind direction during the study period (December 2014 to August 2015) were monitored by a weather station belonging to the *Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina* (Epagri; Ciram, [2015?]), located in Chapecó, 13 km from the study area.

2.2. Study species

Three deciduous native pioneer species with anemochorous dispersal that naturally occur in the seasonal deciduous forest were studied: *Apuleia leiocarpa* (Vogel) J. F. Macbr., *Peltophorum dubium* (Spreng.) Taub., and *Jacaranda micrantha* Cham. *Apuleia leiocarpa* and *P. dubium*, known by the common names of *grapia* and *canafistula*, respectively. They have ornamental and economic importance due to their wood qualities (Carvalho, 2003; Sobral et al., 2013). Both species belong to the Fabaceae family (Carvalho, 2003; Felippi et al., 2012) and their dispersal units are fruits, which are flattened and winged, and classified as samaroid legumes (Filardi et al., 2009). The fructification period of *A. leiocarpa* in the state of Santa Catarina occurs from November to April (Simioni & Belotti, 2009), while that of *P. dubium* from June to August (Carvalho, 2003; Simioni & Belotti, 2009). *Jacaranda micrantha* (Bignoniaceae), known by the common name of *caroba*, is important for its ornamental, medicinal and economic value (Carvalho, 2003; Sobral et al., 2013). *J. micrantha* diaspores are seeds, which are light, winged and flattened (Carvalho, 2003), and the fructification period of this species in Santa Catarina occurs between June and September (Carvalho, 2003; Simioni & Belotti, 2009). The three species are found in the emergent layer of the seasonal deciduous forest of the National Forest of Chapecó. The criteria for plant selection were: 1) adult trees, characterized by their reproductive activity; and 2) the isolation of the plant in the area, to avoid collecting seeds from other neighboring plants.

2.3. Experimental design

The diaspore dispersal was evaluated separately for each species, according to their reproductive phenology. Five adult plants of each species (*A. leiocarpa*, *P. dubium* and *J. micrantha*) were examined in the reproductive stage; which was identified by the presence of flowers and fruits. Three collectors were positioned in line for each plant at 1, 10 and 20 m from the

stem in each of the four cardinal directions so that a total of 12 collectors were installed around each plant. Diaspore collectors of 1 m² were made of wood and nylon mesh (1 mm) and installed at 90 cm above the soil. The collectors were checked weekly during the entire dispersal period and all material deposited on it was collected and taken to the laboratory, where the number of diaspores was recorded. This number was consequently used to calculate the diaspore density at different distances and cardinal directions. The experimental period extended from December 2014 to August 2015.

Tree height was estimated by visually comparing the distance between the tree base and the tree top to an object of known height (10 m) (Durigan, 2003), while the average crown spread was obtained by measuring the longest and shortest extent of the crown (Blozan, 2006). Finally, we measured the length and width of one hundred diaspores found in the collectors to characterize their mean size. Length was measured from the base to the apex of the diaspore, and width was measured at their middle region.

2.4. Data analysis

A two-way analysis of variance (Anova) was performed for each species to test the effects of the distance (1, 10 and 20 m) and direction (North, South, East and West) on diaspore density. Twenty replicates (collectors) were used to evaluate the influence of distance from the mother plant and five replicates were used to evaluate the effect of direction. The Tukey test ($p < 0.05$) was used to compare the mean results. The correlation between plant height or crown spread and seed density in each distance and direction was also performed for each species using the Pearson correlation test ($p < 0.05$). Considering that the wind direction differed between the months, we separately performed One-way Anova for each species to test the differences between the directions in each month ($p < 0.05$). Statistical analyses were developed in the SigmaPlot version 12 software program.

3. RESULTS

The greatest accumulated precipitation during the study period was in July 2015, followed by January and June; the highest average wind speed (47 km/h) in this period was recorded in January (Figure 2). The wind prevailed in the East-Southeast (ESE) direction from December to February, and in the East direction from March to June; wind in in east-northeast (ENE) was recorded only in August (Figure 2).

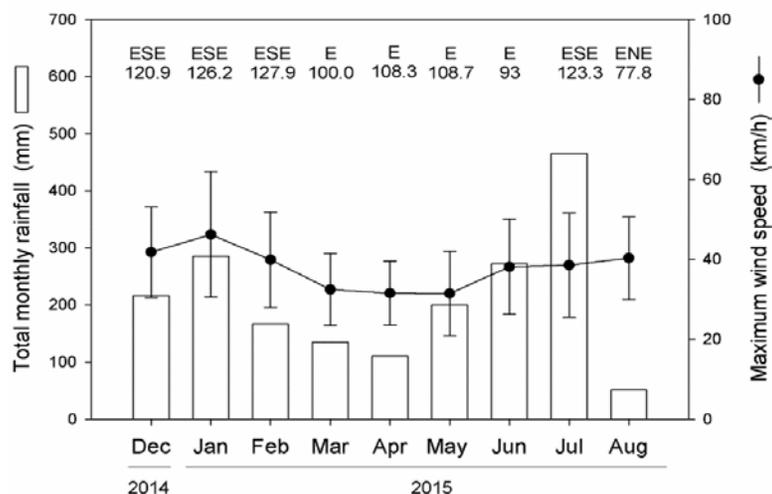


Figure 2. Total monthly rainfall (mm), maximum wind speed (km/h) and wind traits (cardinal direction and degrees) in the municipality of Chapecó during the study period.

The columns represent accumulated monthly precipitation (mm) and the points indicate the average values of the maximum wind speed. The bars indicate standard deviation. E: east, ESE: east-southeast, ENE: wind in east-northeast.

A. leiocarpa diaspore dispersal began in December 2014 with a peak in January (64% of the diaspores), followed by a large decrease in February (Figure 3a). Dispersal ended in April, when no diaspores were found in the collectors (Figure 3a). A total of 2.553 diaspores were recorded over the 134 days of the dispersal period. A density of 73 diaspores/m² were recorded at 1 m from the mother plant, 41 diaspores/m² at 10 m, and 13 diaspores/m² at 20 m.

The dispersal period of *P. dubium* lasted from January to August 2015, with a peak in March (21% of the dispersal), followed by a small decline the next month, and then remaining constant until June. A second dispersal peak was observed in July, before ending completely in August (Figure 3b). A total of 3.364 diaspores were collected for 204 days. The densities were 128 diaspores/m² at 1 m from the mother plant, 31 diaspores/m² at 10 m, and 9 diaspores/m² at 20 m from the mother plant.

The dispersal period for *J. micrantha* extended from April to August 2015, and the dispersal peak was observed in May (63%). A sharp reduction in dispersal was observed in June and it ended completely in August (Figure 3c). The dispersal period lasted for approximately 127 days in which 4,748 diaspores were collected, with densities of 126 diaspores/m² at 1 m, 75 diaspores/m² at 10 m, and 36 diaspores/m² at 20 m from the mother plant.

The dispersal peak of *A. leiocarpa* was observed in January, coinciding with the month of high wind speed and precipitation, which may have contributed to greater synchronization in the abscission of its diaspores (Figures 2 and 3). On the other hand, the dispersal period of *P. dubium* coincided with a reduction in the wind speed, which may explain its longer diaspore dispersal period (Figures 2 and 3).

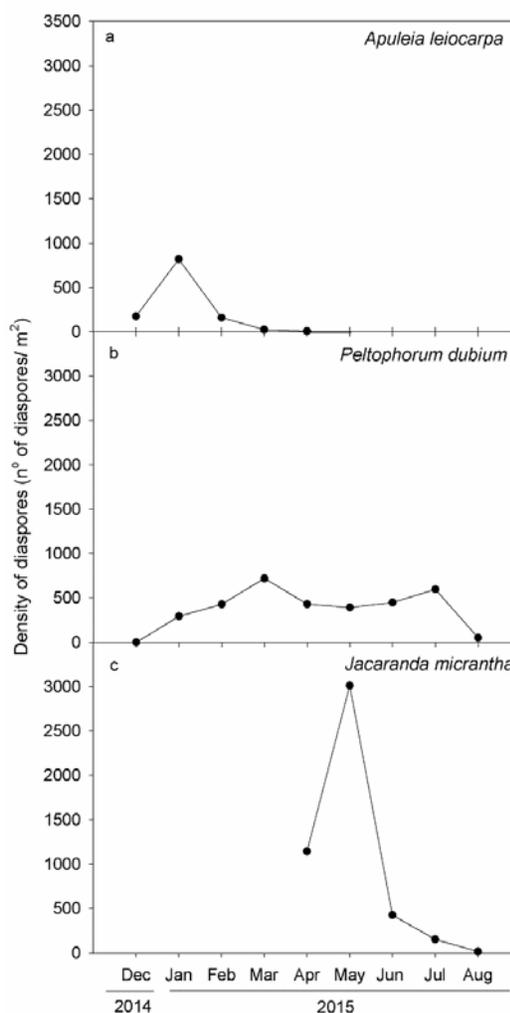


Figure 3. Diaspore density of *Apuleia leiocarpa*, *Peltophorum dubium* and *Jacaranda micrantha* collected monthly in the National Forest of Chapecó between December 2014 and August 2015.

There was no interaction between the distance from the mother plant and cardinal directions regarding diaspore density in any of the studied species ($p > 0.05$). When the factors were evaluated separately, we observed higher diaspore density of the three species near the mother plant, which decreased with increasing distance from the mother plant (Figures 4a, 4c, 4e). *Apuleia leiocarpa* and *J. micrantha* exhibited more diaspores at 1 m than at 10 m, which in turn was higher than the amount collected at 20 m ($p < 0.05$) (Figures 4a, 4e). The amount of

P. dubium diaspores dispersed at 10 m and 20 m was similar, but lower than those collected at 1 m from the mother plant (Figure 4c). The diaspore dispersal was not influenced by the cardinal directions ($p > 0.05$) (Figures 4b, 4d, 4f). The means varied between 40 ± 30.7 and 47.1 ± 28.6 for *A. leiocarpa*, 51.1 ± 92.5 and 62.6 ± 94.6 for *P. dubium*, and 74.2 ± 43.1 and 86.5 ± 42.3 for *J. micrantha*. No differences were observed between the cardinal directions for any species, even when the dispersal was evaluated in each month separately ($p > 0.05$) (Figure 5).

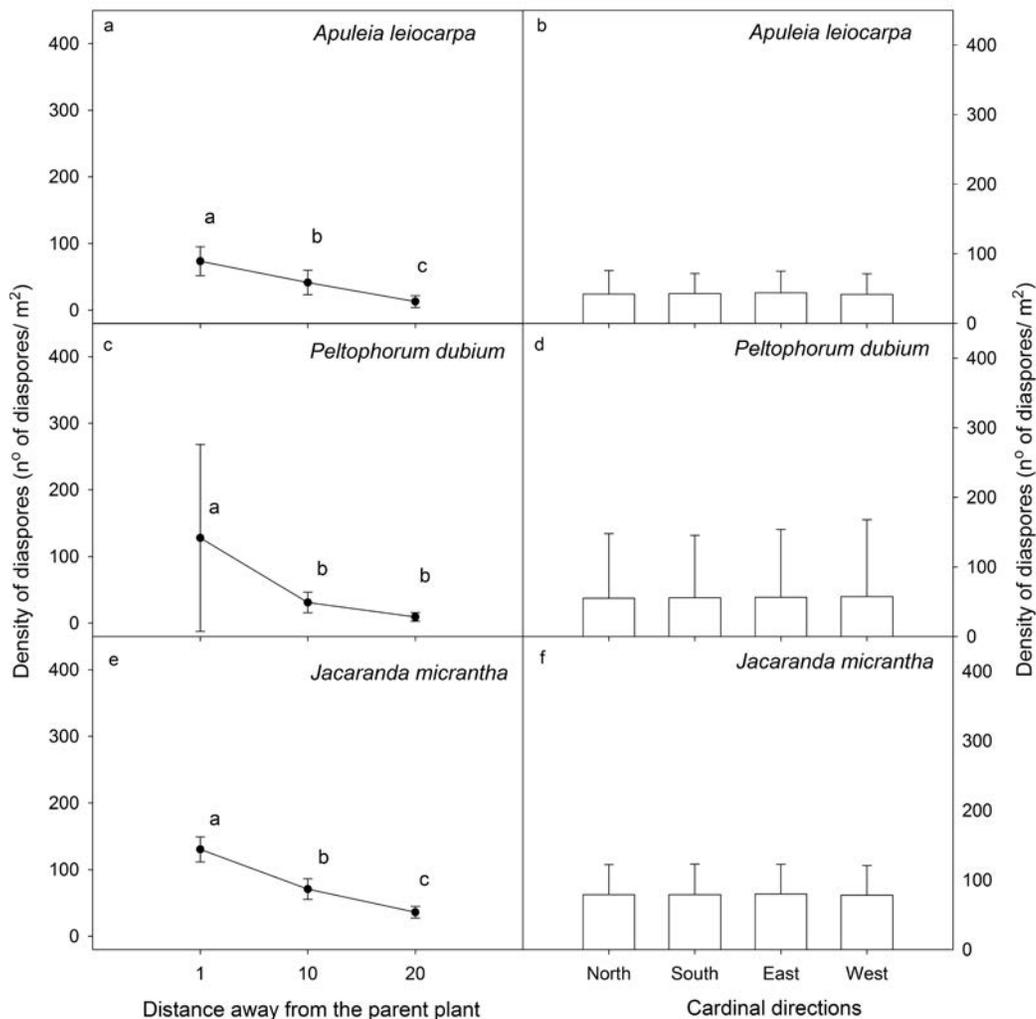


Figure 4. Density of diaspores (number of diaspores/m² ± standard deviation) of *Apuleia leiocarpa* (a and b), *Peltophorum dubium* (c and d), and *Jacaranda micrantha* (e and f) as a function of distance from the mother plant (a, c, and e) and the cardinal directions (b, d, and f) in the National Forest of Chapecó.

The absence of letters indicates the lack of significant difference, and distinct letters show significant differences between means by the Tukey test ($p > 0.05$).

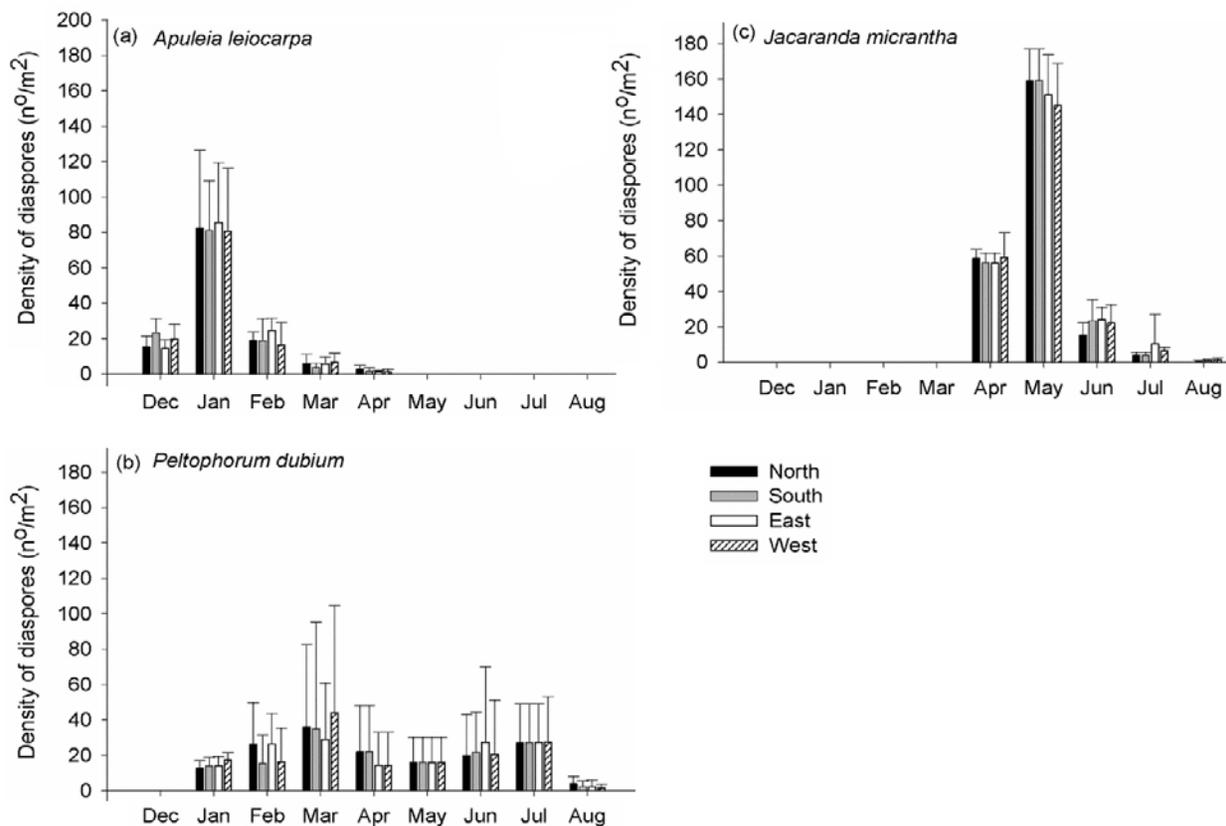


Figure 5. Density (number of diaspores/m²) and standard deviation of *Apuleia leiocarpa* (a), *Peltophorum dubium* (b), and *Jacaranda micrantha* (c) diaspores in the cardinal direction in each month along the dispersal period in the National Forest of Chapecó.

The absence of letters indicates the lack of significant difference, and distinct letters show significant differences between means by the Tukey test ($p > 0.05$).

Negative correlations were observed for dispersal of *A. leiocarpa* diaspores in relation to both the height of the mother plant and the crown spread, so that the higher the plant height and the crown spread, the lower the number of diaspores dispersed at 1 and 10 m. The number of diaspores at 20 m from the mother plant was only influenced by the height of the mother plant. *P. dubium* and *J. micrantha* dispersal were

not influenced either by the height of the mother plant nor by the crown spread (Table 1).

The length and width of diaspores differed among the species. *Peltophorum dubium* diaspores (fruits) exhibited the highest lengths, followed by *A. leiocarpa* and *J. micrantha*. On the other hand, *A. leiocarpa* diaspores (fruits) exhibited the highest width (Table 2).

Table 1. Pearson correlation coefficients and p-values (in parenthesis) of the relationship between plant height, crown spread, total diaspore density, distance from the mother plant and cardinal directions for *Apuleia leiocarpa*, *Peltophorum dubium* and *Jacaranda micrantha* dispersal in the National Forest of Chapecó.

	<i>Apuleia leiocarpa</i>		<i>Peltophorum dubium</i>		<i>Jacaranda micrantha</i>	
	Plant height	Crown spread	Plant height	Crown spread	Plant height	Crown spread
Density (n°/m ²)	0.77 (0.13)	0.80 (0.11)	0.34 (0.58)	0.01 (0.88)	0.51 (0.38)	< 0.01 (1.00)
1 m	-0.74 (< 0.01)	-0.81 (< 0.01)	0.31 (0.19)	0.11 (0.64)	0.22 (0.36)	0.11 (0.65)
10 m	-0.48 (0.03)	-0.51 (0.02)	0.40 (0.08)	0.05 (0.83)	0.04 (0.88)	0.05 (0.85)
20 m	-0.54 (0.01)	-0.43 (0.06)	0.34 (0.14)	0.01 (0.97)	0.03 (0.06)	0.15 (0.53)
North	-0.35 (0.21)	-0.43 (0.06)	0.16 (0.56)	0.06 (0.84)	0.06 (0.84)	0.06 (0.84)
South	-0.34 (0.22)	-0.43 (0.06)	0.14 (0.63)	0.10 (0.72)	0.06 (0.83)	0.26 (0.35)
East	-0.36 (0.19)	-0.43 (0.06)	0.18 (0.53)	0.07 (0.81)	0.08 (0.77)	0.02 (0.94)
West	-0.29 (0.29)	-0.37 (0.17)	0.23 (0.42)	0.01 (0.98)	0.02 (0.93)	0.30 (0.27)

Bold values indicate significant results by Pearson Correlation analysis ($p < 0.05$).

Table 2. Mean length and width and standard deviation of *Apuleia leiocarpa*, *Peltophorum dubium*, and *Jacaranda micrantha* diaspores collected in the National Forest of Chapecó during the 2014/2015 dispersal period. Total diaspores by species = 100.

Species	Length (cm)	Width (cm)
<i>Apuleia leiocarpa</i>	4.0 ± 0.35 [§]	2.04 ± 0.32
<i>Peltophorum dubium</i>	7.3 ± 1.03	1.9 ± 0.26
<i>Jacaranda micrantha</i>	2.25 ± 0.19	1.5 ± 0.04

[§] Mean ± standard deviation.

4. DISCUSSION

Although the diaspores of the three studied species share the characteristics of being winged and flattened, there was variation in diaspore size. The length of *P. dubium* diaspores was almost twice as high than the length of *A. leiocarpa* diaspores, which in turn were also almost twice as high than the length of *J. micrantha* diaspores. However, these diaspore traits do not seem to influence the diaspore dispersal of these species, as all of them showed a higher number of diaspores near the mother plant.

Adaptations of anemochorous diaspores increase the probability of dispersal to areas which are distant from the mother plant (Augsburger, 1986). However, in our study we observed that most diaspores were deposited under or near the canopy of the mother plant. Such accumulation of diaspores near the mother plant, as observed for the three species studied herein, is commonly reported for a great number of plant species, regardless of their dispersal mechanism (Almeida-Cortez, 2004; Clark et al., 2005). Regarding anemochorous species, Lopes et al. (2010) also observed a decline in the density of diaspores with distance from the mother plant, regardless of their morphological adaptations.

The dispersal units of *A. leiocarpa* and *P. dubium* are fruits classified as samaroid legumes (Filardi et al., 2009), which have pericarp projections to aid in anemochorous dispersal, whereas the dispersal units of *J. micrantha* are the seeds themselves, which have tegument expansions (called wings) to aid in dispersal. Moreover, *Apuleia leiocarpa* and *P. dubium* fruits may also be dispersed both by barochory and by anemochory (Carvalho, 2003). Thus, we expected that *J. micrantha* seeds would present more seeds at 10 and 20 m than at 1 m from the mother plant, whereas *A. leiocarpa* and *P. dubium* would present a higher number of fruits at 1 m from the mother plant. Contrary to our expectations, *J. micrantha* presented higher diaspore density at 1 m than at 10 and 20 m from the mother plant, similar to those observed for the other two species.

The seed dispersal distance for some species may be more strongly correlated with the plant than with diaspore traits (Augsburger et al., 2017; Thomson et al., 2011). Indeed, the dispersal of *A. leiocarpa* diaspores in our study was more influenced by plant traits (height and crown spread) than by diaspore size. The height and the crown spread of the mother plant negatively affected the diaspore dispersal of this species. However, we did not observe such influence for the other two species.

In addition to the diaspores and plant traits, dispersal is also influenced by environmental factors such as wind traits and the surrounding vegetation. In order to facilitate the dispersal of diaspores far from the mother plant, anemochorous species must reach a great height and emerge from the forest canopy to gain exposure to the winds that are practically non-existent in a continuous canopy (Horn et al., 2001). Although *Apuleia leiocarpa*, *P. dubium*, and *J. micrantha* are emerging species of seasonal forests (Lindenmaier & Budke, 2006), their heights may not have been sufficient to place these species in the emergent layer of the forest. The *Apuleia leiocarpa*, *P. dubium*, and *J. micrantha* plants sampled in this study presented mean heights of 20.6 ± 1.5, 23.6 ± 2.4 and 18.6 ± 1.9 m (means ± standard deviation), respectively; however, according to Lorenzi (1992) and Sobral et al. (2013), such species can reach heights of between 35 and 40 m. Thus, the higher diaspore density observed near the mother plant for the studied species in the National Forest of Chapecó is possibly related to both the low tree height of plants and to the proximity of arboreal individuals of non-deciduous species which form physical barriers that decrease the effectiveness of the dispersal vector (wind) (Fenner, 1985).

Although variations were observed in the predominant direction of the wind during the study period, we recorded no preferential distribution of the diaspores of any species in any cardinal direction. This observation may also be related to the density of plants (i.e. a greater number of physical barriers against the wind action) in the National Forest of Chapecó, as many plant species from the Seasonal Forests of Southern Brazil tend to exhibit aggregated distribution (Loregian et al., 2012; Sühs & Budke, 2012).

The diaspore dispersal of *P. dubium* and *J. micrantha* occurred simultaneously among the individuals of each species as diaspores were found in all collectors during the dispersal period of each species. The dispersal of *P. dubium* extended for a longer period than expected based on previous studies (Carvalho, 2003; Simioni & Belotti, 2009). The dispersion timing as well as month of occurrence are associated with dispersion vector availability. In the case of anemochorous species such as those studied herein, wind is the primary vector. It is responsible for both the separation of diaspores

from the mother plant and the subsequent dispersal to distant locations (Greene, 2005). Thus, the abscission of certain anemochorous diaspores may be conditioned by the occurrence of winds which are strong enough to cause such separation (Augspurger & Franson, 1987; Deminicus et al., 2009). The dispersal of *P. dubium* diaspores occurred in the period of reduced wind speed in the region, and as such this may have contributed to the longer diaspore dispersal time observed in this study. According to Durigan et al. (1997), *P. dubium* fruits are dispersed slowly by the wind and the ripe fruits remain in the trees for an extended time, as observed in this study. On the other hand, *A. leiocarpa* showed maximum dispersion in January, when higher wind speeds and precipitation probably contributed to the greater synchronization in diaspore abscission.

5. CONCLUSION

Our results showed that the diaspore density of *A. leiocarpa*, *P. dubium*, and *J. micrantha* decrease with the increase in distance from the mother plant. Diaspore sizes of these plants were not related to their dispersal distances. Diaspore dispersal of *A. leiocarpa* was negatively correlated to the plant height and the crown spread. The spatial distribution of diaspores was not influenced by wind direction.

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