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Individual crop size increases predispersal predation by beetles in a tropical palm

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Short Communication

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Abstract

Predispersal seed predation is one of the main causes of seed mortality in plant populations, contributing to decreased plant recruitment. Seed loss has previously been found to be related to crop size. Thus, we examined the influence of individual crop size on predispersal seed predation by beetles in the palm *Syagrus flexuosa* in the Brazilian savanna. The study was carried out in three tropical woodland savanna sites, where we sampled the total seed crop of 46 fruiting palms and checked the presence of beetle larvae inside all seeds per plant. We observed predispersal seed predation of *S. flexuosa* from all sites and a high variation in the number of seeds preyed on per individual palm. Crop size had a positive influence on the number of seeds lost to predispersal seed predators. Variations in levels of predispersal seed predation may also be accounted for by the reproductive phenology of *S. flexuosa*. If fruits are not available at the same time, less resource is available for predators and therefore a high proportion of seeds may be preyed on. Thus, our study demonstrates that an individual plant trait, crop size, is an important predictor of beetle seed damage per palm and a driver of the number of seeds lost to predispersal seed predators.

Introduction

Predispersal seed predation is one of the main causes of seed mortality in plant populations (Janzen, 1969, 1970, 1971a; Zhang et al., 1997; Andersen, 1998; Ramírez and Traveset, 2010), increasing seed limitation and contributing to decrease plant recruitment (Louda, 1982; Kolb et al., 2007). Crop size (the number of seeds produced by an individual plant) and intra- and interpopulational variations may explain some changes in predispersal seed predation (Janzen, 1971a; Traveset, 1995; Crawley, 2000; Xiao et al., 2015; Christianini, 2017).

Predispersal seed predation is mainly performed by specialized invertebrates (Janzen, 1969, 1971a; Kolb et al., 2007; Gripenberg, 2018). Many insects from Coleoptera, Hymenoptera, Diptera, Lepidoptera and Thysanoptera lay their eggs and grow their larvae inside developing fruits and seeds, preying on seeds before dispersal (Janzen, 1969, 1970; Janzen, 1971b; Zhang et al., 1997; Crawley, 2000; Barford et al., 2011). These insects destroy seeds and make fruits less attractive to dispersers (Rathcke and Lacey, 1985), which may limit seed dispersal, plant recruitment and affect the ecological and evolutionary dynamics of their host plants (Kolb et al., 2007). The interest in predispersal seed predation has not matched the significant attention devoted to post-dispersal seed predation over the last few decades, although both are important for the maintenance of tropical plant diversity (Janzen, 1970; Gripenberg, 2018).

Since seeds are critical resources to complete a predator's life cycle, a high number of seeds may allow greater opportunities for oviposition by insects. Therefore, seed predators may exert greater predation pressures where seeds are found in higher densities (density-dependence hypothesis; Janzen, 1969, 1970). On the other hand, a high seed crop size may maximize the probability of satiating local seed predators if many seeds are produced at irregular intervals or are available for only a short period of time (satiation hypothesis; Kelly and Sork, 2002; Kon et al., 2005). In this case, a large seed crop may increase the likelihood of an individual seed reaching maturity even under intense activity of the seed predators (Hubbell, 1980).

Palms (Arecaceae) are present in all tropical and subtropical regions of the world. Most palms and their interactions with insects remain poorly known in tropical ecosystems around the world (Henderson et al., 1995; Prance et al., 2000; Henderson, 2002). Palms are important components (in terms of richness and abundance: Oliveira-Filho et al., 1989; Lenza et al., 2011) of the Brazilian savanna flora, Cerrado. However, less than 50% of flowers of some palm species turn into viable seed due to predispersal seed predation among other reasons (De Steven et al., 1987; Henderson, 2002). Therefore, in this study, we examined the effect of seed crop size variation on seed predation. We expected that higher fruit set would lead to greater predispersal seed predation in a tropical palm species.

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Table 1. Main characteristics of the studied sites in the Cerrado from Central Brazil where predispersal seed predation of *Syagrus flexuosa* was evaluated: Estação Ecológica de Águas Emendadas (ESECAE), Estação Experimental Fazenda Água Limpa (FAL) and Parque Estadual da Serra de Caldas Novas (PESCAN). Dash means lack of information

	ESECAE	FAL	PESCAN
Site coordinates	15°42′–15°38′S 47°33′–47°37′W	15°56′–15°59′S 47°55′–47°58′W	17°46′35.1″–42.7″S 48°40′15″–48°41′ 49.3″W
Elevation (m)	1000–1180	1100	1043
Area (ha)	10,547	4340	12,315
Syagrus flexuosa abundance	–	High and aggregated[a]	High and aggregated[b]

[a]Hay et al. (2000).
[b]Silva et al. (2002).

Materials and methods

Study species

We studied predispersal predation in seeds of *Syagrus flexuosa* (Mart.) Becc., an endemic palm species widely distributed in the Brazilian savanna. The genus *Syagrus* is mostly found in South America, primarily in Brazil (Henderson et al., 1995; Noblick, 2017), and species have been considered fundamental in seasonal ecosystems by offering abundant resources to frugivores in periods of food scarcity (Giombini et al., 2009). This palm flowers between November and April and fruits mainly from July to October (Martins and Filgueiras, 2006). The plant reaches 1–5 m high and it usually has 7–15 green leaves (40–80 pinnate: Noblick, 2017). Flowers are hermaphroditic in 6–12 racemes, with ovoid 4 cm fruits carrying one seed (Mamede, 2008). There are no studies regarding the reproductive biology of *S. flexuosa*, but the congeneric *S. coronata* has been described as self-compatible, with high occurrence of cross-pollination done by bees and beetles (Rocha, 2009).

This study was carried out in three tropical woodland savanna (Cerrado) sites in Brazil: Estação Ecológica de Águas Emendadas (ESECAE, sampled in 2003), Estação Experimental Fazenda Água Limpa (FAL) and Parque Estadual da Serra de Caldas Novas (PESCAN), both sampled in 2012. Study sites are located within conservation areas (distant from each other by at least 45 km) in Central-Western Brazil (Table 1), under Köppen's Aw climate with well-marked rainy (October–March) and dry seasons (April–September) (Nimer, 1989).

Sampling and recording of the predation level

From 7 to 30 palms presenting fruits were sampled *ad libitum* per site (Table 2). In total, 46 palms were sampled (Table 2). Due to logistical reasons, we were unable to survey all sites and plants across the 2 years. All infructescences produced by a palm sampled in each site were collected to record the predispersal seed predation. Infructescences with fruits reaching maturity were recognized through the size and/or colour of fruits. After harvest, each infrutescence was placed in a plastic bag and labelled (site, individual). To evaluate predispersal seed predation, we counted the total number of seeds preyed on per infructescence and per palm individual. We first searched for external signs of predation on seeds (such as holes). To avoid underestimation of insect predation (Andersen, 1998), we also opened all seeds using a scissor in order to verify the presence or not of a larva (an unidentified Curculionidae, Coleoptera). Curculionidae larvae commonly feed on seed endosperm and embryo, complete their life cycle inside seeds and drill an exit hole during fruit ripeness and seed dispersal (Zhang et al., 1997; Crawley, 2000).

Table 2. Average number ± SD of damaged seeds and of individual crop size for *Syagrus flexuosa* at three sites in Central Brazil (*n* = total individuals sampled): Estação Ecológica de Águas Emendadas (ESECAE), Estação Experimental Fazenda Água Limpa (FAL) and Parque Estadual da Serra de Caldas Novas (PESCAN)

Sites	Number of seeds preyed on	Individual crop size
ESECAE (*n* = 7)	29 ± 22	66 ± 39
FAL (*n* = 9)	6 ± 4	30 ± 15
PESCAN (*n* = 30)	4 ± 6	18 ± 4

Data analysis

We applied a Generalized Linear Mixed Model to test for the effects of seed crop on seed predation, using crop size per plant as a fixed predictor variable, palm identification nested within the site as a random factor to control for the spatial distribution of individual palms, pseudo-replication within sites and variation in the number of palms sampled per site. The number of seeds preyed on per palm was the response variable. The model used a Poisson family of error distribution and log-link function. Statistical analysis was done in R (R Core Team, 2013). We used the glmer function to fit the model by maximum likelihood (Laplace approximation) using the lme4 package in R. The full model was compared with a null model containing only an intercept and random effects with analysis of variance. The full model had a better fit to variance in data than expected by random factors only ($X^2 = 11.17$; d.f. = 1; $P = 0.008$). We tested the overdispersion of the full model with an overdispersion detection function suggested by Thomas et al. (2017).

Results

Predispersal seed predation in *S. flexuosa* ranged from 0 to 95% of seeds of individual palms and 35% of all the individuals were not affected by seed predation (Fig. 1). About 24 ± 27% (mean ± SD) of the palm seed crop was lost to predispersal seed predators (although there was a large coefficient of variation of seed loss: 89.1%). We also noticed a great variance in seed crop and loss among sites, with ESECEAE having more predated seeds than the other two areas (Table 2).

Additionally, there was a positive effect of crop size on the number of seeds preyed on per palm (untransformed estimate ±

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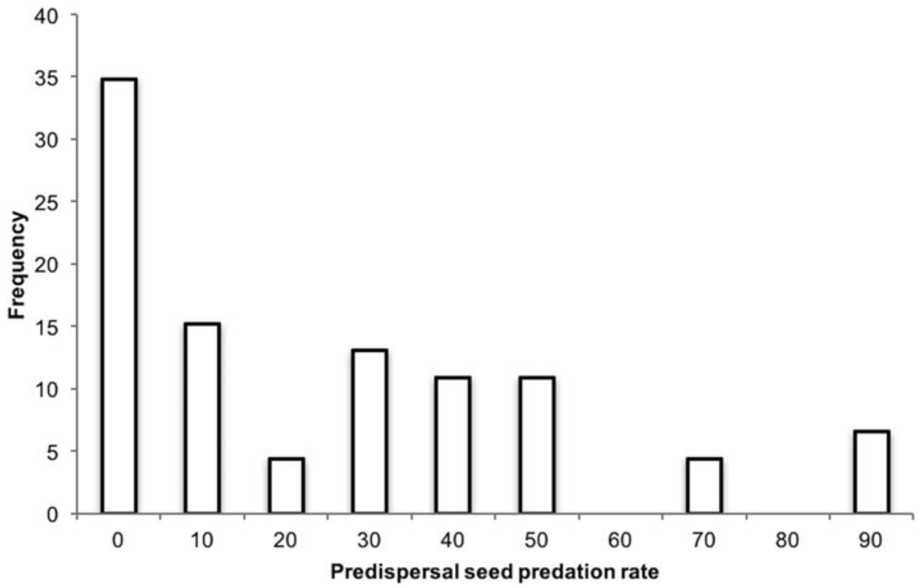

Fig. 1. Distribution of predispersal seed predation rates (predated seeds per total seeds) in *Syagrus flexuosa* individuals. Data are pooled for all individuals in three savanna sites in Central Brazil ($N = 46$).

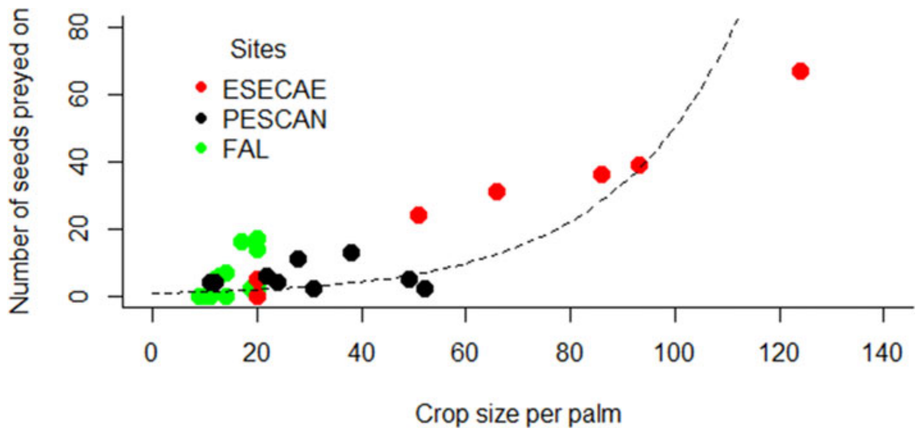

Fig. 2. Predispersal seed predation in response to variation in the number of seeds produced per palm of *Syagrus flexuosa* ($N = 46$). Data are pooled for all individuals in three savanna sites in Central Brazil. Not all points can be seen due to overlap. See the text for details of model fit.

SE: 0.041 ± 0.009; z-value = 4.515; $P < 0.001$; Fig. 2; Model intercept did not differ from zero −0.186 ± 0.387; z-value = −0.480; $P = 0.631$). Since we detected some under dispersion (ratio = 0.254) in our model, the exact value of fixed factor estimates should be interpreted with caution.

Discussion

We observed predispersal seed predation in all sites sampled and a high variation in the number of seeds preyed on per individual of *S. flexuosa*. Although seed losses of the palm species reached a mean of 24% per individual and may suggest a low predation pressure compared with other palms (70% of seed loss), such as *S. romanzoffiana* growing in forest and woodland savanna (Brancalion et al., 2011) and for *Acrocomia aculeata* in savanna (Pereira et al., 2014), there was a large variation among studied individuals. In addition, crop size per palm was a very important driver of the number of seeds lost to predispersal seed predators.

Flower and fruit production in tropical environments are influenced by a multitude of abiotic and biotic factors (Janzen, 1967; Frankie et al., 1974; Mendoza et al., 2017). Several plants from Cerrado show large variations in seed crop among years (Pilon et al., 2015) and *S. fleuxosa* is not an exception. For instance, an average of 87 fruits was produced per palm in 1998 (data not shown) when compared with 30 fruits in 2012 in FAL. This may yield larger seed crops in less predictable time intervals, decreasing the chances to sustain large densities of specialized seed predators and increasing the chances of predator satiation in years of large crops (Kon et al., 2005; Kolb et al., 2007). Despite this, flowering and fruiting of *S. flexuosa* is aseasonal within years in study sites (Bruno et al., 2019). Therefore, insect seed predators may find opportunities for oviposition on seeds of *S. flexuosa* throughout the year. It is possible that female beetles select the most vigorous plants available for oviposition, based on seed crop size, to enhance offspring fitness (Heisswolf et al., 2005). This may explain the increased likelihood of insect seed predation with increases in crop size per palm. Masting flowering/fruiting, on the other hand, could result in predator satiation and in a smaller proportion of seed predation (Kon et al., 2005; Kolb et al., 2007). However, we found no evidence of satiation with increasing crop sizes of *S. flexuosa*. Alternatively, it is possible that less productive plants provide less attractive displays for ovipositing beetles, or that these plants selectively abort infested seeds in early development stages. Future studies could explore this issue further.

This study has shown that predispersal seed predation by Curculionideae larvae is related to the fruit production of *S. flexuosa* in a density-dependent way. The intensity of the seed predation varied more than 15 times among palms considering all sites,

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corroborating other studies with plants from the tropical savanna (Custódio et al., 2014), including palms (Grenha et al., 2008), and increased with the number of fruits produced, indicating that the seed predator's preference for many-flowered individuals may have the potential to affect the selection of plant traits and the overall intensity of seed predation (Kolb et al., 2007).

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