

Reproductive phenology, seed dispersal and seed predation in *Syagrus romanzoffiana* in a highly fragmented landscape

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The aim of this study was to evaluate *Syagrus romanzoffiana* (Arecaceae) (1) reproductive phenology, (2) seed dispersal and (3) seed predation in a highly fragmented landscape. Over a 24-month period, we recorded flowering and fruiting events, proportions of fallen fruit infested by insects, as well as seed dispersal and seed predation by squirrels. Overall flowering and fruiting intensities varied among months; flowering being significantly greater in January and March 2008, and fruiting in April–June and August–September 2008. There were no differences between the first and second years in the flowering and fruiting percentages, flowering and fruiting duration, their peaks or synchrony. The squirrels spent same amounts of time dispersing and eating the seeds. Additionally, there were no statistical differences among the fragments in the numbers of squirrel visits, seeds dispersed or eaten by squirrels, or in the time spent by squirrels on eating or dispersing the seeds. Seed predation rates by insects or percentage of fruits with eggs were not influenced by fruit density, size or weight. *Syagrus romanzoffiana* can be characterized as a robust secondary species, recommended for restoration programs in fragmented landscapes.

Introduction

Phenological studies address the timing of recurring biological processes. For plants, these include reproductive events such as bud formation and flowering, fruiting, and seed germination, along with vegetative processes like leaf flushing and shedding. Phenological events in plants may be affected by biotic and climatic fac-

tors (Van Schaik *et al.* 1993). Environmental cues such as seasonal variations in rainfall, changes in temperature, photoperiod, and irradiance, have been reported as proximate causes triggering phenological events in tropical plants (Wright & Van Schaik 1994). In contrast, biotic factors, such as competition for pollinators or pollinator attraction, competition for seed dispersers, and avoidance of herbivory and seed predation

have been interpreted as ultimate causes responsible for phenological patterns in tropical species (Coley & Barone 1996, Lobo *et al.* 2003). Plant phenology often affects animal populations through temporal changes in resource availability (Sakai *et al.* 1999). Analyses of phenological patterns provide better insight into the dynamics of plant communities, regeneration, temporal resource organization within communities, as well as plant–animal interactions (Van Schaik *et al.* 1993, Talora & Morellato 2000). Seed dispersal and predation affect plant population dynamics and community structure, hence their study is important to management and conservation programs.

In fragmented landscapes, species' abundance and richness become dependent on the size or isolation of the remaining patches (Andr n 1994, Pardini *et al.* 2010). In such cases, many plant–animal interactions may undergo changes that could impair the flower and fruit production, seed dispersal and germination, as well as seedling recruitment. Additionally, these plant–animal interactions are crucial to determining the local communities' structure and dynamics (Scheffer *et al.* 2001). Since nowadays most tropical landscapes are strongly fragmented, the aim of this study was to evaluate the (1) reproductive phenology, (2) seed dispersal, and (3) seed predation of *Syagrus romanzoffiana* ("queen palm" or "Jeriv ", Arecaceae), a palm common in the area (Henderson *et al.* 1995), in a highly fragmented landscape. Over a 24-month period, we recorded (1) intensity, (2) duration (period), (3) peaks, and (4) synchrony of flowering and fruiting. We also registered the proportion of fallen fruits infested by insects, as well as seed dispersal and seed predation by squirrels.

Palm trees produce fruits throughout most of the year, and are therefore an important food source (Terborgh 1986, Henderson 2002), representing 'keystone' species (Terborgh 1986, Pimentel & Tabarelli 2004, Galetti *et al.* 2006). Previous studies indicate that palms are very important to several animals, and their fruits are consumed by a large variety of vertebrates (Paschoal & Galetti 1995, Henderson 2002, Giombini *et al.* 2009). At least to some extent, persistence of frugivore communities depends on this resource (Galetti *et al.* 2001, Keuroghlian & Eaton 2008).

Material and methods

Study area

The study was initially carried out on 31 *S. romanzoffiana* trees distributed in four small fragments (< 100 ha) (Table 1) near Alfenas, south of Minas Gerais, Brazil. The landscape around this city is highly fragmented, with only 4% of the native forest coverage remaining due to the increase of agricultural activities, related mainly to pastures and sugarcane and coffee cultivation (Fundac o SOS Atl ntica & Instituto Nacional de Pesquisas Espaciais 2009). These fragments are inhabited almost exclusively by generalist birds that are poor seed-dispersers (Rabello *et al.* 2010).

Alfenas (21°25'45''S, 45°56'50''W) occupies 848 km², at 880 m a.s.l.. There are 77 500 inhabitants in the area, and the climate is classified as Cwa (K ppen 1948), with hot and humid summers, and dry and cool winters. The annual average temperature is 19.6 °C, and the mean annual precipitation ranges from 1400 to 1700 mm. The vegetation is classified as semi-deciduous Atlantic forest (Veloso 1992).

To test habitat effects, in each fragment, we selected at least three palms located on the fragment edge (up to 5 m from the matrix) and three located in the fragment interior (Table 1); the trees were at least 50 m apart.

Study species

Syagrus romanzoffiana is a secondary species and is common in Argentina, Uruguay, Paraguay, and in central and southeast Brazil in almost all

Table 1. Sizes and coordinates of the four Atlantic forest fragments studied in Alfenas (south of Minas Gerais, Brazil), and the numbers of palms sampled in each fragment.

Fragment	Size (ha)	Lat. (S)	Long. (W)	Number of palms
I	65	21°26'33''	46°09'33''	8
II	52	21°25'20''	46°08'06''	8
III	46	21°28'34''	45°56'12''	6
IV	14	21°27'09''	45°56'50''	9

biomes in the states of Espírito Santo, Rio de Janeiro, Minas Gerais, Goiás and Mato Grosso do Sul (Henderson *et al.* 1995, Henderson 2002). The palm is common in semi-deciduous Atlantic forests, but it is more abundant in fragmented landscapes than in large forest stands (Bernacci *et al.* 2006). It reaches a height of 10–25 m, and its stem is 15–30 cm in diameter. It is commonly used in urban arboriculture (Lorenzi 2002), for food (palm heart and fruits) (Corrêa 1969, Sanchotene 1989), house construction (Lorenzi 2002), and honey production (Souza *et al.* 1994). Flowering and fruiting occurs almost throughout the year, but with greater intensity from February to August. Its fruit are eaten by various vertebrates such as several small rodents, squirrels, agoutis, pacas, coatis, cracids, peccaries, monkeys and tapirs (Galetti *et al.* 1992, Giombini *et al.* 2009). *Syagrus romanzoffiana* is monoecious and has a solitary stem with interfoliar inflorescence consisting of yellow flowers in several rachillae that may reach 32 cm in length; staminate flowers range from 9 to 14 mm in length and have six stamens; pistillate flowers range from 7 to 11 mm in length (Pivari & Forzza 2004). Fruits have soft exocarp and a solid endocarp, approximately 2.5 cm in diameter and weigh (mean \pm SD) 1.62 ± 0.3 g (Galetti *et al.* 1992).

Methods

Phenology

In all fragments, flowering and fruiting of *Syagrus romanzoffiana* was visually evaluated every month during a 24-month period (from September 2007 to August 2009) in plants with a diameter at breast height (DBH) greater than 5 cm. However, for logistical reasons, during the second sampling year, we were not able to sample the six palms in fragment III (situated in a privately-own area). Flowering and fruiting of individual plants were compared in terms of their (1) intensity (*see below*), (2) duration, (3) peak, and (4) synchrony. The phenological comparisons were made between the first (September 2007 to August 2008) and second study year (September 2008 to August 2009, referred to

hereafter as first and second year, respectively).

Depending on the amount of encountered fruits or flowers, an individual plant's flowering or fruiting intensity (I) in a given month, was assigned the following values: 0 if no flowers or fruits present, or 1, 2, 3 or 4 if 1%–25%, 26%–50%, 51%–75% or 76%–100% flowers or fruits present. An overall intensity, I_{overall} , of flowering and fruiting of all plants in each fragment was calculated as follows:

$$I_{\text{overall}} = \frac{\sum_{i=1}^n I_i}{4n} \times 100 (\%)$$

where I is the flowering or fruiting intensity (0 to 4) of plant i in a fragment, n is the total number of the plants in a fragment, and $4n$ is the maximum possible flowering or fruiting intensity value in a fragment, i.e. I of every plant in a fragment equals 4.

Flowering and fruiting percentages are the percentages of individuals in the population that produced flowers and fruits for at least one month during the study period.

Dates of the phenological events were converted into angles (each month of the 24-month study period corresponding to an interval of 15°), and the average angle indicates the mean date of peak reproductive activity for all individuals.

Synchrony in flowering and fruit production among the palms was examined using the r -vector, whose length can range from 0 (when the phenological activity is distributed evenly throughout the year) to 1 (when the phenological activity is concentrated in a single month or time of the year). This vector indicated how concentrated the activity around the mean date is. The flowering and fruiting peaks (average angle) and synchrony (r -vector) were calculated using circular statistics (Morellato *et al.* 2000) in the Oriana software (Kovach 2002).

Seed dispersion and predation

Sciurus ingrami is a small squirrel species occurring in the Atlantic forests (*Mata Atlantica*) from Bahia (northeast Brazil) to Rio Grande do Sul (south Brazil) (Emmons & Feer 1990). It feeds on fruits and seeds, and is the main eater of *S.*

romanzoffiana seeds (Galetti *et al.* 1992, Fleury & Galetti 2006). The squirrel feeds on the seed endosperm leaving triangular teeth marks on it (Bordignon *et al.* 1996).

In each fragment, at least once a month we observed each palm for 30 minutes between 8:00 and 16:00 to record (i) the number of squirrel visits on a palm, (ii) the number of dispersed seeds, (iii) the number of seeds eaten, and (iv) time spent by squirrels on feeding. We also recorded (a) whether the seeds were eaten on the ground or on the palm, and (b) whether not eaten seeds were buried or left on the ground. In total, we gathered the data from 35 palms.

All fruits recently dropped below each marked palm were collected monthly in order to quantify the seed predation rate by insects, mainly coleopterous, one of the most important groups of palm seed predators (Fleury & Galetti 2006). Ten fruits were gathered to identify the emergent adult predator, and 20 fruits were measured and weighed, and their seed predation rates were quantified. The rates of predation were estimated based on the number of seeds with emergence holes or larvae inside them.

Data analysis

Phenology

The monthly intensity of phenological events was compared using split-plot ANOVA (repeated measures in time) followed by the ScottKnott post-hoc test. Flowering and fruiting percentages, duration, peak, synchrony, palm diameter at breast height (DBH) and height of palms were compared between years using nested ANOVA. In nested ANOVA, the factors tested were year (fixed factor), palm (nested within habitat [edge, interior]), and flowering and fruiting percentages, duration, peak and synchrony (nested within year, within habitat [edge, interior]). The normality and homoscedascity of all the data were verified.

Seed dispersion and predation

Fruit density, size and weight were related with

the rate of squirrel seed predation by multiple linear regressions. The differences in numbers of squirrel visits, dispersed and predated seeds, the time spent predated and dispersing, and rates of seed predation by insects were tested with nested ANOVA (Zar 1996). In nested ANOVA, the factors tested were the fragments (fixed factor), the palms (nested within habitat [edge, interior]), and the data for seed dispersion and predation (nested within palms, within habitat [edge, interior]). Fragments and palms (randomly sampled) were tested against the corresponding next lower hierarchical level (Sokal & Rohlf 1995). The palms and fragments were considered random effects.

Results

Phenology

We studied 31 palms in the first year and 25 in the second. The average DBH and height (mean \pm SD) were 18.7 ± 2.8 cm and 12.1 ± 2.1 m, respectively. Palms in both habitats (edge and interior) flowered and produced fruit practically throughout the entire 24-month study period. In the first year, the flowering and fruiting peaks occurred from January to March and from April to May, respectively. In the second year, flowering peaks occurred in October, February and April, and fruiting peaks occurred from September to October. Overall flowering and fruiting intensities (I_{overall} ; Fig. 1) varied among months (split-plot ANOVA: $F_{23,92} = 3.93$, $p > 0.001$ and $F_{23,92} = 6.54$, $p > 0.001$, respectively); flowering being significantly greater in January and March 2008, and fruiting being significantly greater in April–June and August–September 2008 (ScottKnott test: $p < 0.05$).

There were no differences between the first and second years in the flowering and fruiting percentages (nested ANOVA: $F_{2,10} = 2.76$, $p = 0.11$ and $F_{2,10} = 1.89$, $p = 0.20$, respectively), flowering and fruiting duration ($F_{2,34} = 2.76$, $p = 0.08$ and $F_{2,50} = 1.21$, $p = 0.31$, respectively), peaks ($F_{2,34} = 0.38$, $p = 0.69$ and $F_{2,50} = 7.04$, $p = 0.20$, respectively) or flowering and fruiting synchrony (nested ANOVA: $F_{2,10} = 1.45$, $p = 0.28$; $F_{2,10} = 2.02$, $p = 0.18$, respectively) (Table 2).

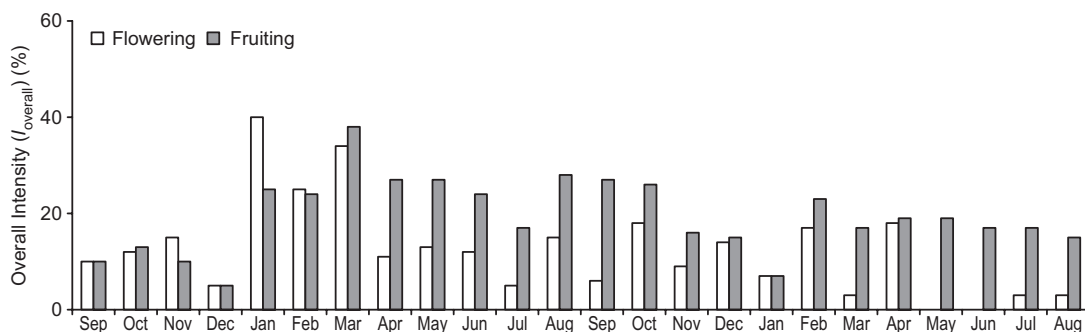


Fig. 1. Overall intensity of flowering and fruiting of *Syagrus romanzoffiana* from September 2007 to August 2009 in fragmented habitats in Alfenas, Minas Gerais, Brazil.

Seed dispersal and predation by squirrels

In fragments III and IV, squirrels were not observed directly, and we found no signs of their presence (teeth marks on fruits on the ground around the palms). Squirrels were encountered during only 8% of the observations. In 2008, the highest squirrel presence occurred in August and December, when the *S. romanzoffiana* fruit production and maturation were at its highest.

In 2009, when the palms did not produce mature fruits (Fig. 1), the squirrels' activity was very low. It took 2 min (± 0.5) for a squirrel to return to the palm after carrying and burying the seeds.

The squirrels spent same amounts of time dispersing and eating the seeds (Table 3). Additionally, there were no statistical differences among the fragments in the numbers of squirrel visits (nested ANOVA: $F_{2,13} = 0.51$, $p = 0.60$), seeds dispersed ($F_{2,16} = 2.23$, $p = 0.14$) or eaten

Table 2. Flowering and fruiting patterns of *Syagrus romanzoffiana* for the total study period (24 months) and for each study year. The percentage of flowering or fruiting, average duration, angle (peak month) or average date and vector of concentration were not significantly different (nested ANOVA) between the years.

	Flowering	Fruiting
Entire study period		
Number of palm trees	25	25
Percentage (number)	88.0 (22)	100.0 (25)
Mean \pm SD duration	3.9 \pm 2.7	14.0 \pm 5.1
Peak month ($^{\circ}$)*	89.00 $^{\circ}$	142.46 $^{\circ}$
Average date of peak reproductive activity	27 Feb. 2008	14 June 2008
Synchrony (r -vector)	0.34	0.22
First year		
Number of palm trees	31	31
Percentage (number)	80.6 (25)	93.5 (29)
Mean \pm SD duration	2.7 \pm 2.2	7.2 \pm 2.8
Peak month ($^{\circ}$)*	143.79 $^{\circ}$	243.78 $^{\circ}$
Average date of peak reproductive activity	23 Jan. 2008	5 Apr. 2008
Synchrony (r -vector)	0.42	0.38
Second year		
Number of palm trees	25	25
Percentage (number)	52.0 (13)	100.0 (25)
Mean \pm SD duration	2.7 \pm 2.0	6.5 \pm 3.2
Peak month ($^{\circ}$)*	99.73 $^{\circ}$	135.79 $^{\circ}$
Average date of peak reproductive activity	12 Oct. 2008	15 Jan. 2009
Synchrony (r -vector)	0.28	0.14

* each month of the 24-month study period corresponds to an interval of 15 $^{\circ}$.

by squirrels ($F_{2,16} = 1.3, p = 0.30$), or in the time spent by squirrels on eating ($F_{2,16} = 1.7, p = 0.19$) or dispersing ($F_{2,16} = 2.4, p = 0.12$) the seeds (Table 3).

Seed predation by insects

There were a total of 2781 fruits, of which only 5.0% ($\pm 6.7\%$ SD) were damaged by insects. The number of fruits collected below each individual palm for multiple linear regression analysis ranged from 12 to 150 (mean \pm SD = 35 ± 3.6). The mean (\pm SD) fruit length, width and weight were 2.6 (± 0.3) cm; 1.8 (± 0.3) cm and 4.4 (± 1.6) g, respectively. Only fruits that showed partial loss of pulp contained insect eggs. The maximum number of eggs and coleopterous larvae in one fruit were 8 and 1, respectively. Seed predation rates ($r^2 = 0.27, p = 0.83$) or percentage of fruits with eggs ($r^2 = 0.29, p = 0.21$) were not influenced by fruit density, size and weight.

Discussion

Phenology

In the present study, *S. romanzoffiana* produced flowers and fruits throughout the entire study period. The results thus support the Newstrom *et al.* (1994) classification of *S. romanzoffiana* as a species with continuous flower and fruit production. *Syagrus romanzoffiana* produced more flowers during the rainy season, and similar patterns have been described for several tropical palm species (De Steven *et al.* 1987, Scariot & Lleras 1991, Ratsirarson & Silander 1996,

Martén & Quesada 2001, Quevedo 2007), and particularly in the Atlantic forest (Rosa *et al.* 1998, Mantovani & Morellato 2000, Mikich & Silva 2001, Voeks 2002).

In the present study, intensity of fruiting was low during the rainy season (September–February), and the peak of fruit production in the first year occurred during the dry season. In many earlier studies, high fruit production in various species was recorded during the rainy season (Rathcke & Lacey 1985, Peres 1994, Rosa *et al.* 1998, Galetti *et al.* 1999, Chapman *et al.* 2005), while some species of palms were found to produce fruits during the dry season (Sist 1989, Peres 1994, Henderson 2002, Miller 2002). However, the phenology of *S. romanzoffiana* as described in the present study differed from that in a large and shaded forest (> 500 ha; Genini *et al.* 2009) where its flowering and fruiting intensity was lower and flowering seasonality greater (September to December) (*see* Genini *et al.* 2009). There was no annual variation in the reproductive phenology of *S. romanzoffiana* in the present study, but such variation was found in a large fragment (1430 ha) by Begnini (2008). In the present study, the duration of flowering of *S. romanzoffiana* was longer and fruiting peaked at different time as compared with those in a larger forest fragment (806 ha; *see* Genini *et al.* 2009).

Seed dispersal and predation by squirrels

Seed dispersal and predation by squirrels were high from August to November 2008, a period of high seed production. In 2009, as the fruit production of *S. romanzoffiana* was low, there were fewer squirrels consuming its fruits.

Fleury and Galetti (2006), comparing *S. romanzoffiana* seed predation by squirrels among forest fragments of different sizes, verified that there was no seed predation in the smaller ones (9.5 and 13 ha). In the present study, seed predation by squirrels was not observed in the small fragments (8 and 10 ha). Furthermore, the two larger fragments (42.8 and 63.3 ha), did not seem to support a high squirrel density as there was little seed predation even during the high seed-production period. Forest fragmentation may

Table 3. Mean \pm SD number of squirrel (*Sciurus ingrami*) visits, dispersed seeds, seed predated and time (min) spent on the dispersal and predation of *Syagrus romanzoffiana* seeds.

Visits	13.0 \pm 1.9
Dispersed seeds	60.0 \pm 9.2
Predated seeds	54.3 \pm 12
Time dispersing	18.8 \pm 34
Time predated	18.4 \pm 53

expose the squirrels to competition with generalist species, such as *Didelphis* sp. (Anderson & Boutin 2002), result in their higher mortality, cause greater difficulty in nest construction and affect their movements inside the fragment (Carey *et al.* 1999). Verboom and Van Apeldoorn (1990) found that squirrels are more frequently observed in areas near large forest fragments.

Seed predation by insects

The rates of seed predation by coleopterous insects were not related to the density, size or height of the fruits. This may be due to the small size of the studied fragments. Many studies about palms presented rates of seed predation by insects higher than 15% (Pizo *et al.* 2006, Salm 2006, Grenha *et al.* 2008) and some higher than 60% (Ramos *et al.* 2001, Pires & Crisostomo 2005). The largest fragment in the present study was 65 ha, while the cited studies were conducted in fragments of at least 400 ha. Many studies demonstrated reduction in seed predation rates by insects in small forest fragments (Janzen 1978, Burkey 1993, Wright & Duber 2001, Cascante *et al.* 2002, Chacoff *et al.* 2004), probably due to edge effect (Chacoff *et al.* 2004). However, Marques *et al.* (2010), who studied the same four fragments from May 2008 to April 2009, found no differences in litterfall, soil moisture, canopy openness or minimum and maximum temperature between the edge and the interior, which suggests that some other factors affect the insects' behaviour.

The amount of pulp in fruits may also limit seed predation by insects. Many studies found effects of fruit manipulation by vertebrates on seed predation by invertebrates (Pizo *et al.* 2006, Rios & Pacheco 2006, Salm 2006). Silvius and Fragoso (2002), reported that in *Attalea maripa* (Arecaceae) partial pulp removal increased the seed susceptibility to predation by Bruchidae (coleopterous insects).

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