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Passage Through *Artibeus lituratus* (Olfers, 1818) Increases Germination of *Cecropia pachystachya* (Urticaceae) Seeds

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Abstract

Neotropical frugivorous bats are common seed dispersers of several pioneer plant species, conferring to the bats an important role for conservation purposes. However, the effects of bats on seed germination have been scarcely addressed. Here, we evaluate effects of passage of seeds through guts of *Artibeus lituratus* bats on the germination of the pioneer tree *Cecropia pachystachya*, accounting for seed storage time and fruit maturity as covariates. To control for seed sources, we collected infructescences and offered them partially to captive bats in order to obtain seeds passed through bats and seeds unpassed from the same infructescences. We then stored in glycerol subsets of seeds of both treatments through time until the beginning of the germination experiment. Germination success responded to storage time and fruit maturation stage. Among seeds from unripe fruits, those passed through the bat guts showed higher percentage of germination than seeds unpassed, but no difference occurred between treatments for seeds from mature fruits. In addition, passage through bats positively affected germination speed, irrespective of fruit maturity. Overall results support that bats can promote germination of *C. pachystachya* seeds, in addition to seed dispersal.

Keywords

bats in captivity, fruit maturation stage, gut passage, pioneer trees, Cerrado

Introduction

Seeds ingested by bats can be spread far from their mother plants when defecated in flight or in the bats' feeding roosts (Charles-Dominique, 1986; Morrison, 1978), decreasing competition among seedlings and the likelihood of attack by pathogens or predators. On a single night, neotropical frugivorous bats can disperse seeds from several forest patches in different stages of plant succession, contributing to a mosaic of species among sites (Munin, Fischer, & Gonçalves, 2012; Vleut, Levy-Tacher, Galindo-González, & de Boer, 2015). Another benefit of being dispersed by bats is the colonization of new sites (Heithaus, 1982), which is likely associate with the predominance of pioneers among bat-dispersed plant species (Lobova, Mori, Blanchard, Peckham, & Charles-Dominique, 2003; Mello, 2002; Munin et al., 2012; Muscarella & Fleming, 2007).

Pioneer tree species commonly are short-lived (<20 years) and exhibit high population densities, clustered occurrences and high rates of endogamy (Kageyama et al., 2003). Each fruit or infructescence can yield hundreds of small seeds with variable time of postdispersal dormancy (irregular dormancy), thus germinating

over extended periods (Goodale et al., 2012). Storage time and viability of seeds in the soil may influence the dynamics of plant communities and the processes of forest regeneration and recovery (Golos, Dixon, & Erickson, 2016). Long time in soil seed banks can, in turn, reduce the likelihood of germination and increase chances of death by seed consumers and stochastic events (Mendes et al., 2015). For instance, *Cecropia pachystachya* Trec. (Urticaceae) seeds stored in soil can keep viability up to 5 years (Charles-Dominique, 1986; Holthuijzen

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& Boerboom, 1982), but storage time of *Cecropia* seeds is often as short as 10 days in the presence of seed consumers (Garcia-Orth & Martínez-Ramos, 2008).

For *Cecropia* species this time is much shorter, in a few days (< 10 days) 100 percent of the seeds can be predated by granivores or killed by pathogens (Garcia-Orth & Martínez-Ramos, 2008). Each fruit or infructescence can yield hundreds of small seeds with variable time of dormancy (irregular dormancy), thus germinating over extended periods (Goodale et al., 2012). Seed storage and viability in the soil influence the dynamics of plant communities and the processes of forest regeneration and recovery (Golos, Dixon, & Erickson, 2016). Storage time of pioneer seeds is variable; up to five years for *Cecropia pachystachya* Trec. (Urticaceae), for instance (Charles-Dominique, 1986; Holthuijzen & Boerboom, 1982). Long time in soil seed banks can, in turn, reduce the likelihood of germination and increase chances of death by stochastic events (Mendes et al., 2015).

Fruits of about 15 *Cecropia* species are eaten by roughly 32 bat species (Horsley, Bicknell, Lim, & Ammerman, 2015; Lobova et al., 2003). *Cecropia pachystachya* (Urticaceae) has characteristics that facilitate seed dispersal by bats (Sánchez, Giannini, & Barquez, 2012). Its sweet fruits with a soft pericarp are key resource for neotropical frugivores, given its year-round availability, a trait shared by other chiropterochoric plants (Marques & Fischer, 2009; Mello, 2002; Munin, Costa, & Fischer, 2011). Several frugivorous can compete for consuming *C. pachystachya* fruits, mainly during low availability of other sources in the dry season, when bats can feed on unripe fruits (Fleming, 1986; Munin et al., 2012; F. C. Passos & Gracioli, 2004).

The genus *Artibeus* includes the largest frugivorous bats of the Neotropics, which most frequently feeds on fruits of *Ficus* spp. (Moraceae) and *Cecropia* spp. (Novaes & Nobre, 2009; F. C. Passos & Gracioli, 2004; J. G. Passos & Passamani, 2003). *Artibeus lituratus* (Olfers, 1818) has been described as a specialist in *Cecropia* fruits (Fleming & Williams, 1990; Howell & Burch, 1974; Sato, Passos, & Nogueira, 2008). However, despite the great abundance and wide distribution of *A. lituratus*, little is known about its influence on germination of *Cecropia* seeds. Moreover, most experiments on effects of passage through bats for seed germination have not employed seeds in the control treatment that are physiologically similar to seeds from bat stools (Cáceres & Monteiro-Filho, 2007; Sato et al., 2008; Teixeira, Corrêa, & Fischer, 2009). Here, we address the role of passage through bats on germination of seeds of the pioneer *C. pachystachya* and took into account storage time and maturation stages of seeds, covariates known to influence germination. We hypothesized that, under equivalent conditions of storage time and fruit maturation, seeds passed through the digestive tract of *A. lituratus* exhibit higher germination success than unpassed seeds.

Methods

Field Site

To run experiments in laboratory, we conducted bat captures and collections of *C. pachystachya* fruits in eight Cerrado fragments (6 to 178 ha) in the urban area of Campo Grande, capital of Mato Grosso do Sul state, southwestern Brazil. Climate is tropical, Aw of Köppen, with a cold dry season (May–August) and hot rainy season (December–March). Mean annual rainfall is 1,500 mm approximately, and mean annual temperature between 20°C and 22°C (INPE-SONDA, 2016). Campo Grande is immersed in the Cerrado Brazilian domain, and it is naturally inhabited by *Artibeus lituratus* and *Cecropia pachystachya* (Ferreira, Fischer, & Pulchério-Leite, 2010).

Bat Captivity and Seed Collection

We mistnetted bats on eight nights per month between March and August 2009 from 6:00 p.m. to 12:00 a.m. Each of the eight fragments was sampled one night per month with six mist nets (3 × 12 m), totaling a 10,368 m² h effort (Munin et al., 2012). Specimens of *A. lituratus*—the most abundant bat species in Campo Grande (Ferreira et al., 2010)—were kept in captivity for the experiment, excluding pregnant females and reproductive males, which exhibit high roost fidelity (Munõz-Romo, Herrera, & Kunz, 2008). We kept bats in 15 steel cages (50 × 20 × 15 cm) installed in the laboratory. These procedures complied with permit SISBIO 20403 issued by the Instituto Chico Mendes (The license for captive collection and maintenance can be found on page <https://www.ibama.gov.br/sisbio>). Each cage housed three females and one male, as the species performs small harems in nature (Munõz-Romo et al., 2008). Before experiments, bats were acclimated to captivity for at least 30 days. Throughout the whole period in captivity (2–7 months), they had access to water ad libitum and were fed with a mixture of 90% fresh fruits, 3% animal protein (dry *Gammarus lacustris*, Sars, 1863), and 7% fibers (Barnard, 1995). We daily provided each cage with 400 g of this mixture and daily cleaned the cages with sodium hypochlorite at 2%. Individuals were weighed every 2 weeks and those showing weight loss or signs of low vitality were released and substituted during the experiment. Before releasing, bats showing low vigor were submitted to a quarantine with caloric supplementation and veterinary monitoring.

On the same nights of bat captures, we collected infructescences from 10 *C. pachystachya* trees growing in urban areas, at least 900 m distant from each other. Greenish infructescences exhibiting a rigid consistency were considered unripe and those with other coloration that easily exposed seeds by handling were considered ripe. To obtain seeds passed through bat guts, we roughly offered 400 g of *C. pachystachya* fruits, either ripe or

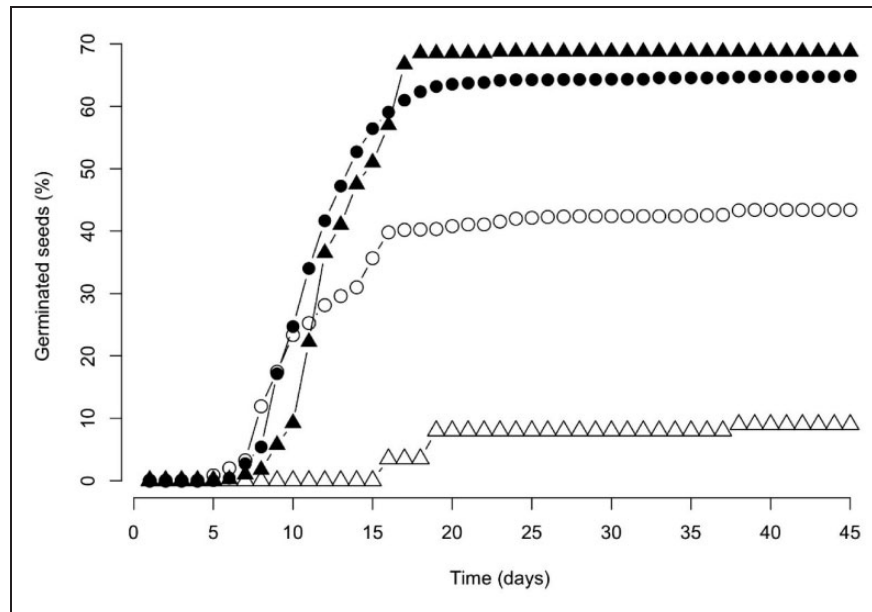


Figure 1. Germination of *Cecropia pachystachya* (Urticaceae) seeds according to different treatments: from ripe or unripe fruits (solid and hollow symbols, respectively), passed or unpassed (circles and triangles, respectively) through guts of *Artibeus lituratus* (Phyllostomidae) bats.

unripe (randomly selected), to each cage during intermittent days, and collected seeds from stools in the next morning. For each day of collection, we assembled 100 intact seeds as one subsample and stored it in glycerol. To obtain subsamples of noningested seeds, we additionally collected 100 intact seeds directly from parts of the infructescences offered to the bats, and also stored in glycerol. Thus, we obtained 100-seeds paired subsamples in different dates, and time of storage varied among pairs of subsamples since the collection date until the beginning of the germination experiment. Four treatments that included different storage time among subsamples were established—seeds from ripe fruits passed through bats, seeds from ripe fruits unpassed, seeds from unripe fruits passed through bats, and seeds from unripe fruits unpassed. Storage in glycerol avoids stimulation of germination by external factors, and it can reveal how germination capacity of *C. pachystachya* seeds may change through time.

Germination Experiment and Analyses

For the germination experiment, all glycerol-stored seeds were initially washed and sterilized in a 2% sodium hypochlorite solution for 10 min. Only seeds with viable embryos were included. Embryo viability was evaluated by testing 20% of the seeds in each 100-seed subsample with 2,3,5-triphenyltetrazolium chloride. Seeds of each subsample were then transferred to individual Petri dishes lined with filter paper soaked in distilled water. Petri dishes were kept in a germination chamber controlled for photoperiod (12 h light and 12 h dark) and temperature

(25°C) during 45 days. Germinated seeds were recorded every 24 h and promptly discarded; germination was considered when seeds exhibited the radicle.

To assess the germination pattern, we used the time elapsed until germination onset, the germination speed, and the percentage of germinated seeds per subsample. For each subsample, the time until germination onset was defined as the number of days required for the first seed to protrude the radicle. To measure germination speed, we used the ratio between number of germinated seeds and number of days until the germination curve became asymptotic. Multivariate analysis of covariance (Pillai's trace test) was used to evaluate the effects of storage time, fruit maturation stage (ripe or unripe), and seed source (passed or unpassed through bats) on germination.

Results

Passage through *A. lituratus* bats increased germination of *C. pachystachya* seeds by 40%. The germination percentage of unpassed seeds from unripe fruits was less than 10%, much lower than for the other seed treatments (Figure 1). Seeds from ripe fruits presented similar germination success for passed (65%) or unpassed (69%) seeds. Seeds from unripe fruits that passed through bats germinated as fast as seeds from ripe fruits (6.67 days of experiment, on average; Table 1). Germination speed and percentage were higher for seeds from ripe than unripe fruits, but no difference occurred between gut-passed and unpassed seeds.

The storage time of seeds ranged from 34 to 123 days among subsamples. The storage time, fruit maturation stage, and seed source (passed or unpassed through bat

Table 1. Means and Standard Deviations of Germination Percentage, Time to Germination Onset, and Germination Speed Among 100-Seeds Trials of *Cecropia pachystachya* (Urticaceae) Seeds From Ripe or Unripe Fruits, Which Passed or Unpassed Through Guts of *Artibeus lituratus* (Phyllostomidae) Bats.

| Fruit stage | Germinated seeds (%) | Time to germination onset (days) | Germination speed (%/day) |
|-----------------------------|---------------------------------|----------------------------------|---------------------------------|
| Seeds passed through bats | | | |
| Ripe ($n = 22$) | $65^a \pm 14.2$ | $8^a \pm 1.7$ | $4^a \pm 1.1$ |
| Unripe ($n = 15$) | $43^b \pm 28.1$ | $7^a \pm 1.8$ | $2^b \pm 1.7$ |
| Seeds unpassed through bats | | | |
| Ripe ($n = 4$) | $69^a \pm 40.0$ | $9^a \pm 2.65$ | $4^a \pm 2.8$ |
| Unripe ($n = 2$)* | 9 ± 2.8 | 16 ± 0.0 | 0.4 ± 0.28 |
| ANOVA results | | | |
| | $F(2,38) = 4.66,$ $p = .047$ | $F(2,38) = 1.92,$ $p = .483$ | $F(2,38) = 4.72,$ $p = .044$ |

Note. Means followed by same letters in the same columns do not differ (Tukey HSD, $\alpha = .05$). Probabilities are Bonferroni-corrected for repeated tests.

*Excluded from ANOVA.

Table 2. Results of Multivariate Analysis of Covariance (MANCOVA) for Germination of *Cecropia pachystachya* (Urticaceae) Seeds Passed and Unpassed Through Guts of *Artibeus lituratus* (Phyllostomidae) Bats.

| Independent variables | Pillai trace | F | Gl | p |
|------------------------------------|--------------|---------|----------|--------|
| Seed source | 0.489 | 10.5561 | 3 and 33 | <.001 |
| Storage time | 0.240 | 3.484 | 3 and 33 | .02657 |
| Maturity stage | 0.310 | 4.943 | 3 and 33 | .0060 |
| Interactions: | | | | |
| Source and storage time | 0.482 | 10.256 | 3 and 33 | <.001 |
| Source and maturity stage | 0.227 | 3.244 | 3 and 33 | .0342 |
| Storage and maturity stage | 0.088 | 1.071 | 3 and 33 | .3747 |
| Source, storage and maturity stage | 0.0311 | 0.3536 | 3 and 33 | .78682 |

Note. Germination percentage, time to germination onset, and germination speed were the response variables. Seed source (bat feces or mother plant), storage time, and stage of fruit maturity were the independent variables.

guts) influenced germination (Table 2). Seeds from ripe fruits and stored for longer germinated faster, irrespective of germination percentage or time elapsed to germination onset (Figure 2). Among seeds from ripe fruits, germination did not differ between sources, passed or unpassed through bat guts. In contrast, among seeds from unripe fruits, the passage through *A. lituratus* increased the speed and the percentage of germination. Using a covariance analysis model, these germination patterns were significantly explained by all three independent variables investigated—time of seed storage, fruit maturity, and seed source (Table 2).

Discussion

Our results support that passage through the guts of *A. lituratus* bats benefits germination of *C. pachystachya* with regard to speed and percentage, notably for seeds from unripe fruits. Moreover, results demonstrate that fruit maturity and seed storage time affect the germination

process of *C. pachystachya*. Although the role of bats on seed germination has been investigated for different seed species, most experiments have failed to control for the origin (mother plant), fruit maturity, and the time of storage of seeds (Lopez & Vaughan, 2004; Sato et al., 2008; Teixeira et al., 2009; Traveset, 1998). Therefore, our results on *C. pachystachya* seeds point out that germination experiments uncontrolled for fruit maturity and time of seed deserve some caution of interpretation. Speed of seed germination is important for increasing competitiveness through early seedling establishment and for reducing chances of postdispersal predation or attack by pathogens (Fischer, 1997). This way, passage through bat guts can improve the ecological success of dispersed seeds.

The early germination of an increased percentage of seeds from unripe fruits after passage through bats are likely due to bats' digestive enzymes (Baldwin & Whitehead, 2015; Izhaki & Safriel, 1990; Teixeira et al., 2009). Ripe fruits present increased concentration of ethylene, which enhances the action of gibberellins

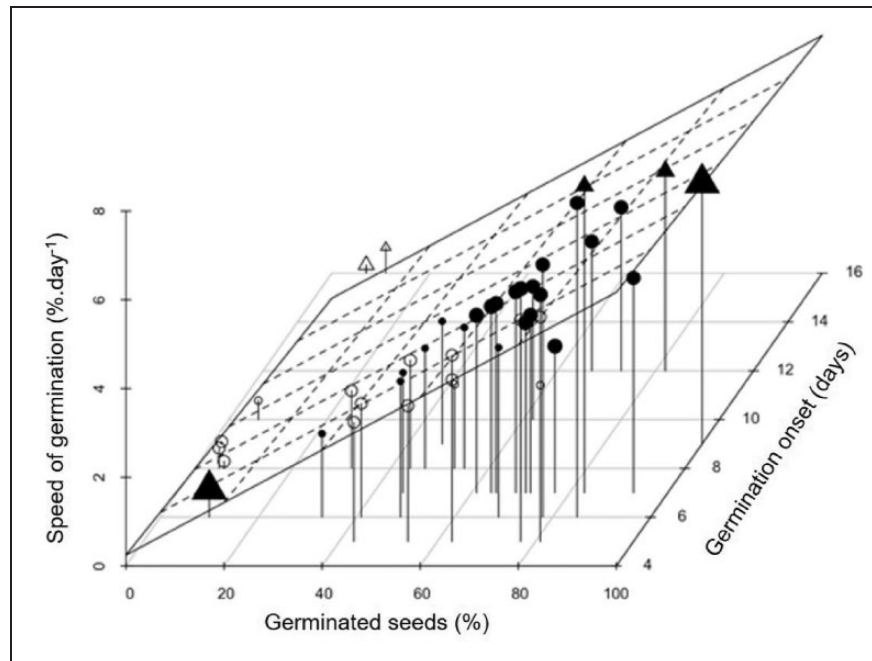


Figure 2. Relationships among speed of germination, percentage of germination and germination onset of *Cecropia pachystachya* (Urticaceae) seeds passed through *Artibeus lituratus* bats' guts (circles) or not passed (triangles), obtained from ripe fruits (filled symbols) or unripe fruits (empty symbols). Size of symbols is proportional to storage time. Note that seeds from ripe fruits germinated faster and in higher percentage than seeds from unripe fruits.

responsible for breaking seed dormancy and promoting germination, thus seeds from mature fruits could germinate early and in high percentages (Corbineau, Xia, Bailly, & El-Maarouf-Bouteau, 2014; Gupta & Chakrabarty, 2013). On the other hand, low concentrations of ethylene in unripe fruits retain the action of gibberellins, constraining stimulus for germination. The digestive enzymes of *A. lituratus* likely boost the action of gibberellins, thus increasing germination of seeds from unripe fruits but not affecting seeds from ripe fruits that already present ethylene-activated gibberellins. By promoting germination of seeds from unripe fruits, *A. lituratus* bats, and likely other Neotropical fruit bats as well, can reduce possible negative effects for plants due to animal consumption of immature fruits. Availability of fruit sources for frugivores can be limited in disturbed sites, where *C. pachystachya* may be common, and during the dry season in the Brazilian Cerrado. In this situation of low fruit availability, competition for resources may increase among frugivores, forcing them to resort to alternative or unripe fruits (Munin et al., 2012; F. C. Passos & Gracioli, 2004; Teixeira et al., 2009). Under this circumstance, passage through bats can compensate for the low germinating ability of seeds from immature fruits of *C. pachystachya*.

Seed dispersal and germination events depend on different factors associated to environmental conditions and to the seed vectors and eaters, which may vary in space and time. Thus, the success of such events frequently are related to where and when they occur (Fischer, 1997;

Izhaki & Safriel, 1990). The positively photoblastic seeds of *C. pachystachya*, and of other tropical pioneer trees as well, are benefited in open vegetation after disturbances (Goodale et al., 2012). *Artibeus lituratus* and other Neotropical frugivorous bats commonly forage in disturbed areas as they feed on fruits of several pioneer trees and shrubs (Charles-Dominique, 1986; Ferreira et al., 2010; Mello, 2002; Munin et al., 2012; Novaes & Nobre, 2009; F. C. Passos & Gracioli, 2004; J. G. Passos & Passamani, 2003), so they are suitable vectors for seeds arriving in regenerating patches. On one hand, seeds of pioneer plants dispersed to open areas need to germinate fast because the early successional stages are ephemerals and the first established seedlings have increased chances to grow up to adult size (Fleming & Williams, 1990). Therefore, the increased germination speed provided by passage through the bats' guts is likely positive for *C. pachystachya* seeds arriving in disturbed sites.

On the other hand, strategies of pioneer plants may include the dispersal of seeds widely in old-growth vegetation areas and their maintenance in soil seed banks, anticipating a disturbance event (Holthuijzen & Boerboom, 1982; Lobova et al., 2003). Within this strategy, accelerating germination after passing through the bats might negatively affect the plant reproductive success by reducing the ability of seed dormancy or by causing germination under low availability of light, which may prevent seedling establishment or survival. This possible negative effect for endozoochoric bat-dispersed

pioneer plants is an issue to be addressed. Nonetheless, the year round availability of *C. pachystachya* fruits provides continuous seed dispersal by the bats (Munin et al., 2012; Teixeira et al., 2009), which would compensate a possible reduced longevity in the seed banks.

Implications for Conservation

Under the controlled conditions investigated, *C. pachystachya* germination proved more successful for seeds from ripe fruits, irrespective of gastrointestinal transit, and depended on both storage time and fruit maturation stage. Seed ingestion by bats increased germination, which occurred earlier, faster, and at a higher percentage compared with noningested seeds. By enhancing germination success, particularly of *C. pachystachya* seeds from unripe fruits, in addition to the benefits of seed dispersal, *A. lituratus* plays an increased role for forest regeneration. Our results highlight the importance of controlled experiments as a tool for conservation efforts, given its potential to bridge knowledge gaps identified by studies focused on endozoochory, especially dispersal carried out by bats. Investigations involving germination measurements can be inconclusive without control of seed sources and time of storage, thus failing to clarify the role that different dispersers may play for seed germination. By contributing toward the establishment of numerous plant species via seed dispersal, bats are key species in the mechanism of forest succession (Arroyo-Rodríguez et al., 2015). Understanding the role played by frugivorous bats in germination constitutes an important additional step forward to forest management and conservation, particularly in fragmented areas. The synergy of the dispersal and germination processes associated to fruit bats can promote successful maintenance of pioneer plant populations and the forest regeneration at all.

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Declaration of Conflicting Interests

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