

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/actoec

Original article

Seed predation and fruit damage of *Solanum lycocarpum* (Solanaceae) by rodents in the cerrado of central Brazil

Denis C. Briani^a, Paulo R. Guimarães, Jr.^{b,*}

^aPrograma de Pós-Graduação em Ciências Biológicas (Zoologia), Departamento de Zoologia, Universidade Estadual Paulista (UNESP), Av. 24-A no. 1515, Bela Vista, Rio Claro, SP, 13506-057, Brazil

^bPrograma de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP), Caixa Postal 6109, 13083-970, Campinas, SP, Brazil

ARTICLE INFO

Article history:

Received 13 December 2004

Accepted 11 January 2006

Published online 4 January 2007

Keywords:

Cerrado

Density-dependence

Fruit damage

Solanaceae

ABSTRACT

Although neotropical savannas and grasslands, collectively referred to as cerrado, are rich in seed-eating species of rodents, little is known about seed predation and its determinants in this habitat. In this study, we investigated seed predation and damage to fruits of the widespread shrub *Solanum lycocarpum*. In addition, the influence of two possible determinants (distance from the parental plant and total crop size) on the feeding behaviour of *Oryzomys scotti* (Rodentia, Sigmodontinae) was also examined. *O. scotti* were captured more frequently close to the shrubs or on shrub crops, indicating that these rodents were attracted to the shrubs and that seed predation was probably distance-dependent. Moreover, the proportion of damaged fruit on the plant decreased as the total crop size increased; consequently, more productive plants were attacked proportionally less by rodents. This pattern of fruit damage may reflect predator satiation caused by the consumption of a large amount of pulp. Alternatively, secondary metabolites in *S. lycocarpum* fruits may reduce the pulp consumption per feeding event, thereby limiting the number of fruits damaged.

© 2006 Elsevier Masson SAS. All rights reserved.

1. Introduction

Seed predation by animals is one of the main causes of mortality in higher plants (Hulme, 2002; Hulme and Benkman, 2002). Insects and vertebrates are often able to predate almost all seeds set in a reproductive season (Blate et al., 1998), and high rates of seed predation may play a key role in plant population dynamics (Maron and Simms, 2001) and community structure (Janzen, 1970; Webb and Peart, 1999). Rodents are important seed predators in many habitats, such as neotropical forests (Forget, 1992; Hoch and Adler, 1997; Brewer and

Rejmanek, 1999), temperate, deciduous woodlands (Hulme and Hunt, 1999), mesic grasslands (Edwards and Crawley, 1999), and shortgrass steppes (Hoffmann et al., 1995). Rodents act as pre-dispersal (Hulme, 2002; Fedriani et al., 2004) or post-dispersal (Forget and Milleron, 1991; Hulme, 1994) seed predators, and seed predation by rodents may markedly affect plant reproductive dynamics. Hence, understanding the factors that determine the extent of seed predation is a key aspect in deciphering how seed–animal interactions are organized.

In Neotropical forests, the determinants of post-dispersal seed predation by rodents, especially dasyproctids, have

* Corresponding author.

E-mail address: paulomiudo@uol.com.br

1146-609X/\$ – see front matter © 2006 Elsevier Masson SAS. All rights reserved.

doi:10.1016/j.actao.2006.01.008

been investigated and we now know how factors such as seed size (Jansen et al., 2002), secondary chemistry (Guimarães et al., 2003), presence of pulp (Guimarães et al., 2005), fruit infestation by insects (Silvius, 2002), diaspore burial (Silva and Tabarelli, 2001), distance to the nearest reproductive individual (Wright and Duber, 2001), conspecific adult tree clustering (Forget, 1993; Peres et al., 1997), gestation status of seed-eating rodents (Henry, 1997), and season of the year (Henry, 1999; Peres et al., 1997) can affect this predation. In contrast, the determinants of pre-dispersal seed predation by rodents have generally been overlooked. This is especially true for non-forest habitats, such as the savannas and grasslands in central Brazil, collectively known as *cerrados* (Oliveira and Marquis, 2002), for which little is known about seed predation by invertebrates and vertebrates (Marquis et al., 2002).

In this study, we investigated the interactions between Neotropical rodents and *Solanum lycocarpum* fruits in a region of *cerrado* in central Brazil. *S. lycocarpum* is a conspicuous plant in *cerrados*, where it occurs in natural areas and pastures. In particular, we addressed the following questions: (1) Which rodent species attacked the fruits of *S. lycocarpum* prior to dispersal? (2) Was rodent activity correlated with the proximity of fruiting *S. lycocarpum* shrubs? and (3) How crop size affected the number of fruits that were not attacked by rodents?

2. Material and methods

In June 2002, fieldwork was done in the Reserva Ecológica do IBGE – Instituto Brasileiro de Geografia e Estatística (15°57'S, 47°53'W), a 1.4 ha protected area located in the center of the *cerrado* formation, close to Brasília, in central Brazil (Briani et al., 2004). The climate of this area is markedly seasonal, with a dry season between May and August (<10% of the annual precipitation). The average temperature is 21.9 °C, and the mean annual rainfall is 1469 mm. Typically, *cerrado* vegetation includes an array of vegetation physiognomies, such as grasslands, woodlands, dry forests and evergreen forests (Oliveira-Filho and Ratter, 2002). The areas selected for sampling in this work were located in *cerrado sensu stricto*, and had a total woody plant cover of 40–70%, with scattered trees and shrubs, a canopy generally 5–7 m high and a ground layer with a variable covering of grasses and herbs (see Ratter, 1991 for a detailed description). The rodent species encountered in this study area included *Necromys lasiurus* Lund. (the most abundant species), *Oryzomys scotti* Langguth and Bonvicino, *Thalpomys cerradensis* Hershkovitz, *Thalpomys lasiotis* Thomas, *Calomys tener* Winge, *Calomys callosus* Rengger and *Oligoryzomys microtis* Allen.

2.1. Plant species

Solanum lycocarpum St. Hil. (Solanaceae), locally known as “lobeira”, is a polymorphic species that occurs principally in disturbed areas of the *cerrado* of central Brazil. Plants from central Brazil are 3 m high shrubs with branches covered by prickles and trichomes. Green, hairy, spheroidal fruits are produced all year round and are usually dispersed by mammals such as maned wolves (*Chrysocyon brachyurus*) and cattle (Pott and Pott, 1994). The large fruits weigh up to 750 g and,

after complete ripening, the pulp emits a characteristic smell (Lombardi and Motta, 1993). There are 600–800 suboval, black seeds ($4.0 \pm 1.0 \text{ mm} \times 6.0 \pm 2.0 \text{ mm}$, mean \pm SD) per fruit (Lombardi and Motta, 1993).

2.2. *S. lycocarpum* as an attractant of *Oryzomys scotti*

We examined 12 fruiting individuals of *S. lycocarpum* and sought evidence of seed predation and pulp damage by rodents. Traps to capture small mammals were baited with a slice of fruit containing pulp and seeds and were placed on or close to these 12 fruiting plants. The traps were checked early in the morning and the bait was renewed if necessary. Captured rodents were identified to the species level, weighed and released at the same point of capture. To determine whether rodent activity was correlated with the distance to fruiting *S. lycocarpum* shrubs, three traps were placed at different distances from the closest fruiting *S. lycocarpum* shrub: (i) on the ground, close to the trunk of the plant, (ii) on the ground, 5 m from the plant, and (iii) on the ground, 10 m from the plant. An additional trap was placed 1.5 m high in the crop of the plant. Hence, four traps were used in each plant. Each trap was set for 10 consecutive nights. Fallen fruits were removed to avoid any potential rodent–fruit interaction that could reduce the success of capture. However, we did not remove any fruits from the plants, so as not to introduce excessive bias into the system. Consequently, our trapping success in the fruit crop was probably underestimated.

We calculated the success rate of trapping for each rodent species in each trap. Trapping success rate was defined as the proportion of nights in which at least one individual of a given species was captured. Nights and traps in which other small mammals were captured were not considered when calculating the success rate of a given species. Bootstrapping procedures (10,000 randomizations) were used to generate a 95% confidence interval (CI) for the observed average success of trapping for each of the four distances indicated above. The confidence limits were determined using the percentile method (Manly, 1997). We expected that if rodents were attracted to fruiting shrubs then the trapping success rate would be higher in the fruit crop and close to the shrub than at 10 m from the closest shrub.

The success rate for traps placed close to the same plant was influenced by the particularities of each shrub. To control for the individual effect, we calculated the difference *D* between the trapping success rate close to the trunk of a plant and that of traps 5 m and 10 m from the plant. The resulting values of *D* were averaged for the 12 plants. This analysis was done only for *O. scotti* because the trapping success for the other species was very low (see Section 3). We expected $D > 0$ if *O. scotti* were attracted to the proximity of the shrub. We used resampling methods (10,000 randomizations) and calculated the empirical distribution of *D* by assuming a random trapping success rate for the plant, i.e., the trapping success would be randomized between the two distances for the same plant but not among the plants. If the observed value of *D* was significantly higher than expected by chance after controlling for the effects peculiar to each shrub, then *O. scotti* was

considered to have been attracted to the proximity of *S. lycocarpum*. We did not use the trapping success rate in the fruit crop in this analysis because it was probably underestimated (see above).

2.3. Crop size and damage to fruits by rodents

To test whether crop size affected the number of fruits that escaped attack by rodents, we recorded the crop size (the total number of fruits) and the intact crop size (the number of fruits not damaged by rodents) for each *S. lycocarpum* shrub ($n = 12$). The data were fitted to the power-law function $y = ax^b$ and fitting was done using a log-transformation and a least-square linear regression (according to Harms et al., 2000):

$$\log(y + 1) = b \log(x + 1) + \log a,$$

where x is the recorded crop size at the shrub, y is the intact crop size remaining at the time of observation, and b is the slope representing the rate at which the intact crop size varies relative to the recorded crop size. If $b = 1$, then the proportion of intact fruits is independent of total crop size, whereas if $b > 1$, then the proportion of intact fruits increases with crop size, and if $b < 1$, then the proportion of intact fruits decreases with crop size. The slope was tested with a paired t-test to compare the observed number of intact fruits with the expected value when $b = 1$ (Harms et al., 2000). The expected values were calculated by substituting the b value for 1.

3. Results

Ripe fruits and seeds attacked by rodents showed the same pattern of predation (gnawed) and were found on the ground and on the plants. We captured 77 rodents belonging to three species, namely, *N. lasiurus* (8 records), *C. callosus* (4 records) and *O. scotti* (65 records).

O. scotti were captured more frequently close to the shrubs or on the shrub crops (Fig. 1) while predated on seeds (pre- and post-dispersal) and consuming pulp. Indeed, this species was the only species captured on shrub crops (Fig. 1). The other two species had very low trapping success rates and no clear pattern of variation in relation to the distance from the shrubs. Since the sample sizes for *N. lasiurus* and *C. callosus* were small, only *O. scotti* was used in subsequent analyses. After controlling for individual shrub effects, there was still evidence that *O. scotti* was attracted to *S. lycocarpum*. The observed values of D for the 0–5 m ($D = 0.16$) and 0–10 m ($D = 0.24$) comparisons were significantly higher than expected by the empirical distribution generated by randomization procedures ($P < 0.005$ for both distances).

Crop size varied from 5 to 13 fruits. The number of intact fruits varied markedly among the shrubs (from 25% to 86% of fruits). However, the intact crop size was not proportional to total crop size. The functional relationship between intact and total crop sizes was: $\log(\text{intact crop size}) = -1.09 + 1.26 \times \log(\text{total crop size})$ (least-squared log-log regression, $F = 11.66$, $R^2 = 0.49$, $n = 12$, $P = 0.006$). The observed slope (1.26) was significantly greater than the value of $b = 1$ expected in the case of proportionality (paired t-test, $t = 5.84$, d.f. = 11, $P < 0.001$) (Fig. 2).

4. Discussion

Neotropical savannas and grasslands have a rich fauna of rodents (well-known seed predators) that include more than 50 species, which corresponds to 45% of non-flying mammalian species in these regions (Marinho-Filho et al., 2002). Indeed, at least 33 species of rodents include seeds in their diet, and granivory is especially common in murid rodents (27 spp. > 80% of the species in this family) (Marinho-Filho et al., 2002). Since rodents are often abundant in cerrados (Alho and Pereira, 1985; Ernest and Mares, 1995; Marinho-Filho et al., 2002), seed predation by rodents, especially murid

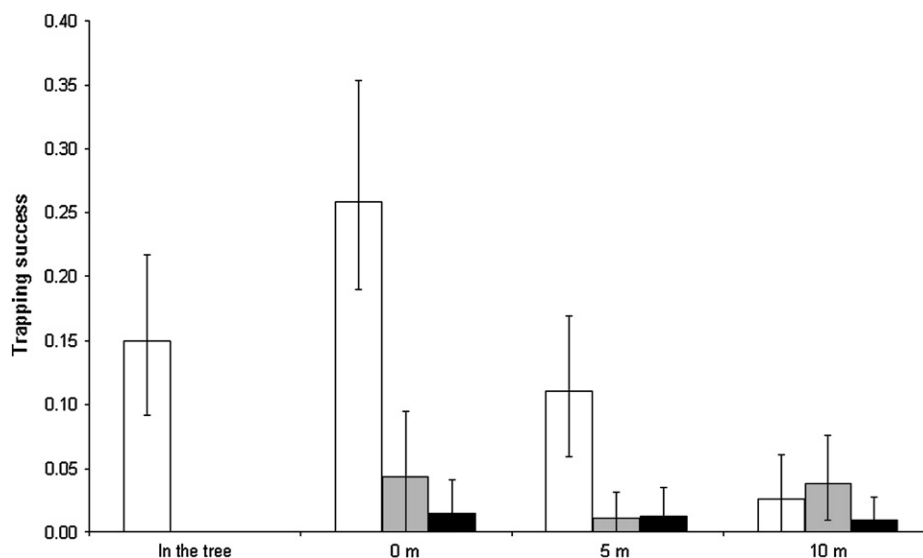


Fig. 1 – The success rate in trapping rodents as a function of distance to the nearest *Solanum lycocarpum* plant. The rodent species are *Oryzomys scotti* (white columns), *Necromys lasiurus* (grey columns) and *Calomys callosus* (black columns). The bars indicate the 95% confidence intervals estimated using bootstrapping procedures.

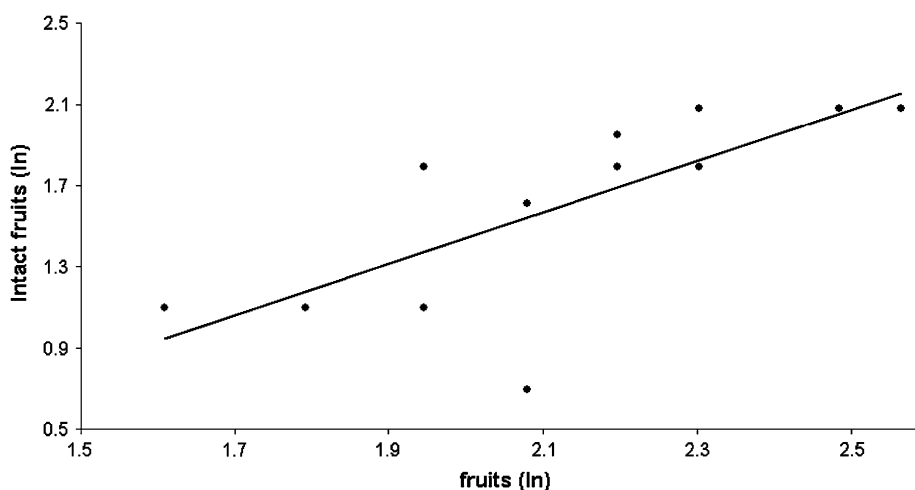


Fig. 2 – The relationship between crop size (number of fruits) and intact crop size of shrubs of *Solanum lycocarpum*. Solid line indicates the power-law that best fits the data. The slope of 1.26 is significantly greater than 1.0, suggesting that larger crop sizes are attacked proportionally less than smaller crops.

rodents, is expected to have profound effects on plant reproductive dynamics.

The results of this study provide evidence of seed predation and pulp consumption of *S. lycocarpum* fruits by rodents, mainly *O. scotti*. Seed predation directly affects plant reproductive success by reducing the total number of seeds that may be recruited (Hulme, 2002). However, seed predation is probably not the most negative impact of rodent attacks. The large fruits of *S. lycocarpum* contain hundreds of small-sized seeds and many seeds are likely to escape rodent consumption. The consequences of damage to the fruit may be potentially the most negative effect of rodent activity for *S. lycocarpum*, which produces only a few large fruits at a time. Such damage may allow pathogens, such as fungi, to attack the pulp, thereby reducing the attractiveness of these fruits to seed dispersers (e.g. Cipollini and Stiles, 1993).

The non-linear relationship between total and intact crop size indicated that the effects of pre-dispersal seed predation by *O. scotti* were not uniform among individuals of *S. lycocarpum*: individuals with larger crops had a lower proportion of damaged fruits than those with smaller crops. We propose two non-mutually exclusive hypotheses to explain the reduction in the proportion of fruits damaged relative to crop size. First, this pattern of damage may reflect predator satiation, as suggested by other studies of seed predation involving rodents (Theimer, 2001; Schnurr et al., 2002; but see Manson et al., 1998). In the *O. scotti*-*S. lycocarpum* system, the consumption of pulp by rodents and the huge fruit size may increase the chances of predator satiation. Second, the high concentration of secondary metabolites in *S. lycocarpum* fruits may inhibit extensive pulp consumption per feeding event, thereby reducing the number of fruits damaged (Cipollini, 2000). Future work should investigate these hypotheses.

Acknowledgments

The Instituto Brasileiro de Geografia e Estatística (IBGE) kindly authorized the fieldwork and provided logistical

support at the IBGE Ecological Reserve (RECOR). This study was partially supported by a Master's degree scholarship from FAPESP to DCB (grant no. 99/03722-8). PRG was also supported by FAPESP. We thank S. Hyslop for editorial assistance and for providing valuable suggestions on earlier drafts of this paper. R. Arditi, M. Hossaert-McKey and two anonymous reviewers provided very useful criticisms of early versions of the manuscript.

REFERENCES

- Alho, C.J.R., Pereira, L.A., 1985. Population ecology of a cerrado rodent community in central Brazil. *Revista Brasileira de Biologia* 45, 597–607.
- Blate, G.M., Peart, D.R., Leighton, M., 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82, 522–538.
- Brewer, S.W., Rejmanek, M., 1999. Small rodents as significant dispersers of tree seeds in a neotropical forest. *Journal of Vegetation Science* 10, 165–174.
- Briani, D.C., Palma, A.R.T., Vieira, E.M., Henriques, R.P.B., 2004. Post-fire succession of small mammals in the cerrado of central Brazil. *Biodiversity and Conservation* 13, 1023–1037.
- Cipollini, M.L., 2000. Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. *Revista Chilena de Historia Natural* 73, 421–440.
- Cipollini, M.L., Stiles, E.W., 1993. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology* 74, 751–762.
- Edwards, G.R., Crawley, M.J., 1999. Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* 118, 288–296.
- Ernest, K.A., Mares, M.A., 1995. Population and community ecology of small mammals in a gallery forest of central Brazil. *Journal of Mammalogy* 76, 750–768.
- Fedriani, J.M., Rey, P.J., Garrido, J.L., Guitian, J., Herrera, C.M., Medrano, M., Sanchez-Lafuente, A.M., Cerda, X., 2004. Geographical variation in the potential of mice to constrain an ant-seed dispersal mutualism. *Oikos* 105, 181–191.
- Forget, P.M., 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24, 408–414.
- Forget, P.M., 1993. Postdispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94, 255–261.

- Forget, P.M., Milleron, T., 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87, 596–599.
- Guimarães, P.R., José, J., Galetti, M., Trigo, J.R., 2003. Quinolizidine alkaloids in *Ormosia arborea* seeds inhibit predation but not caching by agoutis (*Dasyprocta leporina*). *Journal of Chemical Ecology* 29, 1065–1072.
- Guimarães, P.R., Lopes, P.F.M., Lyra M.L., Muriel A.P., 2005. Fleshy pulp enhances the location of *Syagrus romanzoffiana* (Arecaceae) fruits by seed-dispersing rodents in an Atlantic forest in south-eastern Brazil. *Journal of Tropical Ecology* 21, 109–112.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495.
- Henry, O., 1997. The influence of sex and reproductive state on diet preferences of four terrestrial mammals of French Guianan rain forest. *Canadian Journal of Zoology* 75, 929–935.
- Henry, O., 1999. Frugivory and the importance of seeds in the diet of the orange rumped agouti (*Dasyprocta leporina*) in French Guiana. *Journal of Tropical Ecology* 15, 291–300.
- Hoch, G.A., Adler, G.H., 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* 13, 51–58.
- Hoffmann, L.A., Redente, E.F., McEwen, L.C., 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* 5, 200–208.
- Hulme, P.E., 1994. Postdispersal seed predation in grassland – its magnitude and sources of variation. *Journal of Ecology* 82, 645–652.
- Hulme, P.E., 2002. Seed-eaters: dispersal, destruction and demography. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, pp. 257–273.
- Hulme, P.E., Benkman, C.W., 2002. Granivory. In: Herrera, C., Pellmyr, O. (Eds.), *Plant-animal Interactions: An Evolutionary Approach*. Blackwell, Oxford, pp. 132–154.
- Hulme, P.E., Hunt, M.K., 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* 68, 417–428.
- Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J., Van Wieren, S.E., 2002. The role of seed size in dispersal by a scatter-hoarding rodent. In: Levey, D.J., Silva, W., Galetti, M. (Eds.), *Third International Symposium – Workshop on Frugivores and Seed Dispersal: Biodiversity and Conservation Perspectives*. CAB International Press, Oxford, pp. 209–225.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104, 501–528.
- Lombardi, J.A., Motta Jr., J.C., 1993. Seed dispersal of *Solanum lycocarpum* St. Hil. (Solanaceae) by the maned wolf, *Chrysocyon brachyurus* Illiger (Mammalia, Canidae). *Ciência e Cultura* 45, 126–127.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, second ed. Chapman & Hall, London.
- Manson, R.H., Ostfeld, R.S., Canham, C.D., 1998. The effects of tree seed and seedling density on predation rates by rodents in old fields. *Ecoscience* 5, 183–190.
- Marinho-Filho, J., Rodrigues, F.H.G., Juarez, K.M., 2002. The cerrado mammals: diversity, ecology and natural history. In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, pp. 266–284.
- Maron, J.R., Simms, E.L., 2001. Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory. *Journal of Ecology* 89, 578–588.
- Marquis, R.J., Morais, H.C., Diniz, I.R., 2002. Interactions among cerrado plants and their herbivores: unique or typical? In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, pp. 306–328.
- Oliveira, P.S., Marquis, R.J., 2002. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, 398 pp.
- Oliveira-Filho, A.T., Ratter, J.A., 2002. Vegetation physiognomies and woody flora of the cerrado biome. In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, pp. 91–120.
- Peres, C.A., Schiesari, L.C., Diasleme, C.L., 1997. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. *Journal of Tropical Ecology* 13, 69–79.
- Pott, A., Pott, V.J., 1994. *Plantas do Pantanal*. EMBRAPA, 320 pp.
- Ratter, J.A., 1991. *Guia para a vegetação da Fazenda Água Limpa (Brasília, DF), com chave para gêneros lenhosos de dicotiledôneas do cerrado*. Universidade de Brasília, Brasília.
- Schnurr, J.L., Ostfeld, R.S., Canham, C.D., 2002. Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos* 96, 402–410.
- Silva, M.G., Tabarelli, M., 2001. Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. *Acta Oecologia* 22, 259–268.
- Silvius, K.M., 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or ‘grubivory’? *Journal of Tropical Ecology* 18, 707–723.
- Theimer, T.C., 2001. Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. *Journal of Tropical Ecology* 17, 177–189.
- Webb, C.O., Peart, D.R., 1999. Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology* 80, 2006–2017.
- Wright, S.J., Duber, H.C., 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica* 33, 583–595.