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INSIGHTS

The Benefits of Myrmecochory: A Matter of Stature

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ABSTRACT

Myrmecochory, or seed dispersal by ants, occurs widely in angiosperms, and particularly in temperate forest herbs in the northern Hemisphere and sclerophyll shrubs in Mediterranean-climate landscapes. The lipid-rich elaiosome on the seed provides nutrition to the ants; however, how the plant benefits from myrmecochory remains unclear. Here, we provide the first comprehensive analysis of the Euphorbiaceae species in the semi-arid Caatinga vegetation region of northeastern Brazil, and show that myrmecochory strongly associates with small plant stature, even after controlling for seed size. The association of myrmecochory with small stature suggests that the primary benefit to plants concerns distance of dispersal, which reduces parental and sibling competition.

Abstract in Portuguese is available in the online version of this article.

Key words: Caatinga vegetation; directed dispersal; distance dispersal; Euphorbiaceae; plant-ant interactions; seed protection hypothesis.

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Myrmecochory is a common and widespread form of seed dispersal, occurring in 11,000 angiosperm species (4.5% of total) from 334 genera and 77 families (Lengyel *et al.* 2009). A lipid-rich appendage (elaiosome) on the seed attracts ants, who transport the diaspore to the nest, consume the elaiosome, and discard the intact seed, either inside the nest or on an external refuse pile (Beattie 1985). Elaiosome consumption can increase ant colony fitness (Morales & Heithaus 1998, Bono & Heithaus 2002), but the benefit for plants remains a matter of contention.

The proposed benefits of myrmecochory for plants (Beattie 1985, Giladi 2006), include: (1) directed dispersal to ant nests, which provide nutrient-enriched micro-sites more suitable for seed germination than random sites (directed dispersal hypothesis; Beattie 1985, Hanzawa *et al.* 1988); (2) rapid removal and burial as protection against seed predators (predation-avoidance hypothesis; Heithaus 1981, Smith *et al.* 1989) or fire (fire-avoidance hypothesis; Berg 1975, Hughes & Westoby 1992); and (3) distance dispersal as a way of escaping from parental competition and optimizing safe-site location (distance dispersal hypothesis; Andersen 1988a, Higashi *et al.* 1989, Boyd 2001). However, in most cases, the benefit has not been demonstrated empirically. This is remarkable, given the substantial proportion of myrmecochorous angiosperm species and the proposal that myrmecochory significantly drives global diversification of flowering plants (Lengyel *et al.* 2009).

The association of myrmecochory with small plant stature has received little attention (but see Hughes *et al.* 1994). Myrmecochory occurs particularly frequently in temperate forest herbs in the northern Hemisphere (Culver & Beattie 1978, Beattie & Culver 1981), and sclerophyll shrubs of Mediterranean-climate landscapes in South Africa, southern Australia, and southern Europe (Berg 1975, Milewski & Bond 1982, Bond & Slingsby 1983, Westoby *et al.* 1991, Garrido *et al.* 2002). We found only a single published example (*Croton priscus*; Passos & Ferreira 1996) of an arborescent myrmecochore. Here, we examine a largely unrecognized type of myrmecochores—Euphorbiaceae species from Brazilian Caatinga (see Leal *et al.* 2007)—as a powerful test of the generality of the association of myrmecochory with small plant stature. We then discuss the implications of small plant stature for seed dispersal by ants, arguing that it can explain only one of the hypothesized benefits.

METHODS

Caatinga (*sensu* Pennington *et al.* 2009) is a mosaic of Seasonally Dry Tropical Forests and semi-arid scrub vegetation in northeastern Brazil, with an extremely high diversity of Euphorbiaceae (Rodal & Melo 1996). Many of these species—woody plants from the genera *Cnidoscolus*, *Croton*, *Jatropha*, and *Manihot*—are diplochorous, with ballistic discharge of seeds from explosive dehiscent capsules followed by ant removal of their caruncle-bearing seeds (Leal *et al.* 2007, 2014a,b, Lôbo *et al.* 2011). Three of the five Euphorbiaceae subfamilies (Thakur & Patil 2011) include Myrmecochorous genera that grow as trees and shrubs. Information on this group of myrmecochorous plants remains scarce (Lengyel *et al.* 2009, 2010). Non-myrmecochorous euphorbs in Caatinga include bird- and mammal-dispersed species (*e.g.*,

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Alchornea, *Hieronyma*, *Joannesia*, *Omphalea*, *Sapium*), and species with ballistic-dispersed, ecarunculate seeds (*e.g.*, *Acalypha*, *Amanoa*, *Ditaxis*, *Pachystroma*, *Plukenetia*). Natural fire occurs rarely, if ever, in Caatinga (Rizzini 1979, Prado 2003), so protection from fire does not provide a benefit in this system.

We assembled information about the maximum height and seed size of myrmecochorous and non-myrmecochorous plants in Caatinga, using records from the literature or in herbarium collections. We obtained height data for 144 (77%) of the 186 euphorb species known from Caatinga. One potential explanation for myrmecochory's association with small plant stature is that seeds of trees might be too large to be transported by ants. We obtained seed size data for 54 (30%) of the species. We performed one-way ANCOVA with seed dispersal mode as the main factor, plant maximum height as the primary variable, and seed size as a co-variable. Normality of the residuals and homogeneity of variances verified through Shapiro–Wilk and Levene tests, respectively. All procedures are detailed in Zar (1999), and we used R software (R Development Core Team 2008).

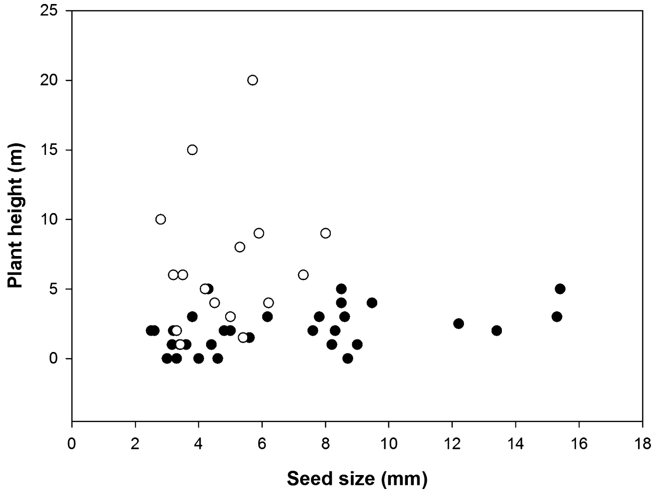

FIGURE 1. Seed size and maximum height of myrmecochorous (black circles; $N = 33$ species) and non-myrmecochorous (white circle; $N = 16$ species) Euphorbiaceae from northeastern Brazil's Caatinga vegetation.

RESULTS

Of the 186 euphorb species known from Caatinga, we identified 116 (68%) as myrmecochorous, including species in the genera *Croton* (58 species), *Manihot* (20), *Euphorbia* (10), *Cnidoscolus* (9), *Sebastiania* (9), *Jatropha* (5), *Mabea* (2), *Stilingia* (2), and *Ricinus* (1). Non-myrmecochorous genera included *Chamaesyce* (12), *Acalypha* (7), *Dalechampia* (7), *Actinostemon* (4), *Alchornea* (4), *Ditaxis* (4), *Sapium* (4), *Gymnanthes* (3), *Amanoa* (2), *Bernardia* (2), *Euphorbia* (2), *Maprounea* (2), *Savia* (2), *Tragia* (2), *Aparisthmium* (1), *Astrocasia* (1), *Caperonia* (1), *Chaetocarpus* (1), *Cleidion* (1), *Hieronyma* (1), *Joannesia* (1), *Mabea* (1), *Margaritaria* (1), *Microstachys* (1), *Omphalea* (1), *Pachystroma* (1), and *Plukenetia* (1).

ANCOVA showed that the incidence of myrmecochory is clearly associated with plant stature: for a given seed size, myrmecochores were always smaller than non-myrmecochores ($F_{(1,46)} = 26.7$; $P < 0.001$; Fig. 1). Additionally, almost 90 percent of myrmecochorous species are woody, whereas non-myrmecochores have a relatively even mix of woody and non-woody species (Fig. 2). Among woody plants, 64 percent of myrmecochorous species have a maximum height of 2 m or less, and the overwhelming majority (95%) have a maximum height 5 m or less (Fig. 3). By contrast, most (58%) non-myrmecochores have a maximum height >6 m (Fig. 3).

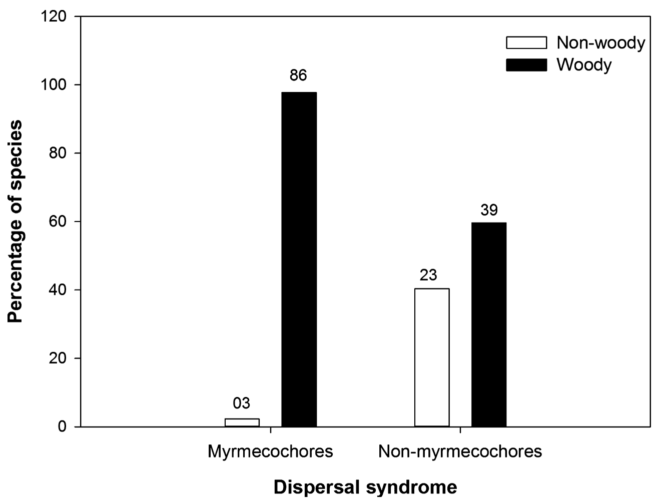

FIGURE 2. Woodiness of myrmecochorous and non-myrmecochorous Euphorbiaceae plants occurring in Caatinga vegetation. Number of species is shown above the bars.

DISCUSSION

Myrmecochory in the extremely diverse Euphorbiaceae of Caatinga vegetation in northeastern Brazil is clearly associated with small plant stature, even after controlling for seed size. This conforms to the small plant stature typical of hotspots of myrmecochore diversity elsewhere (*e.g.*, Beattie & Culver 1981, Milewski & Bond 1982, Bond & Slingsby 1983, Garrido *et al.* 2002). Small plant stature has critical implications for understanding the benefits of myrmecochory.

Directed dispersal.—Soils near ant nests are often enriched in nutrients, which can enhance seedling growth (Culver & Beattie 1983, Andersen 1988b). The concentration of myrmecochory in nutrient-poor Mediterranean heathlands and shrublands makes directed dispersal to nutrient-enriched micro-sites an attractive hypothesis (Beattie 1985). However, it remains unclear why this benefit would exclude trees, especially as a large proportion of tree species have seeds no larger than those of myrmecochorous shrubs and herbs. Moreover, a meta-analysis of the benefits of myrmecochory (Giladi 2006) found that the directed dispersal hypothesis was consistently supported only for tropical forest trees, which are primarily dispersed by vertebrates and only secondarily by ants (Leal & Oliveira 1998, Pizo & Oliveira 2000,

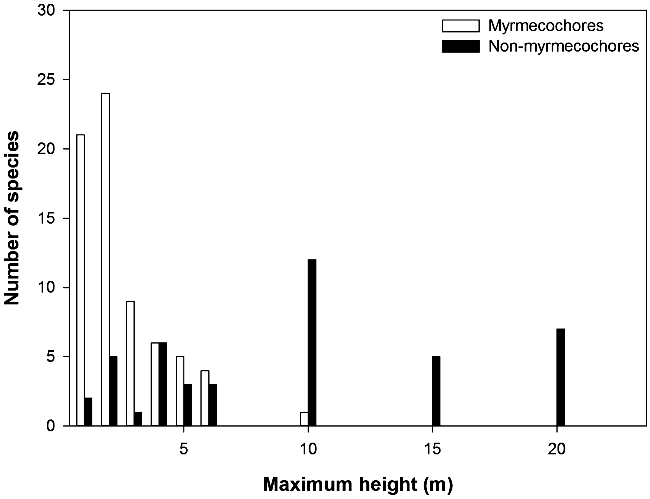

FIGURE 3. Maximum height of myrmecochorous and non-myrmecochorous Euphorbiaceae of the Caatinga vegetation.

Passos & Oliveira 2003). The directed dispersal hypothesis thus cannot explain the association of myrmecochory with small plant stature.

Protection against seed predators.—Plants commonly lose a substantial proportion of post-dispersal seeds to predation; rapid removal and burial by disperser ants likely reduces this loss (Giladi 2006). Although myrmecochory often occurs in habitats that lack large numbers of granivorous rodents (Ohara & Higashi 1987, Hughes & Westoby 1992, Ohkawara *et al.* 1996, Lôbo *et al.* 2011), other seed-eaters such as granivorous ants and beetles (*e.g.*, Ohara & Higashi 1987, Lôbo *et al.* 2011) might prey on seeds. However, as for directed dispersal, the benefit of protection against predators should apply as much to trees as to smaller plants, suggesting that protection from predators cannot explain the association of myrmecochory with small plant stature.

Distance dispersal.—Mean distance dispersal by ants is typically ~2 m (Gómez & Espadaler 1998, 2013). In Caatinga vegetation, it varies from a few centimeters to more than 25 m, with an average of 1–5 m depending on the euphorb species (Leal *et al.* 2007, 2014a,b). Moreover, myrmecochorous dispersal curves tend to be strongly left-skewed, with a tail of dispersal events >10 m in most habitats (Andersen 1988a, Andersen & Morrison 1998, Leal *et al.* 2014a,b). For herbs and shrubs, these seemingly short distances are sufficient to remove seeds from beneath the parent canopy, reducing parent-offspring competition (Westoby *et al.* 1982, Leal *et al.* 2007), locate 'safe' sites for recruitment within established populations (Andersen 1988a), and reduce sibling competition. The reduction of sibling competition might be particularly important for obligate-seeder species that are killed by fire but recruit prolifically afterward.

Of the widely proposed benefits of myrmecochory, only distance dispersal directly relates to plant stature. The distance dispersal hypothesis predicts that myrmecochory will only evolve where the range of seed dispersal by ants exceeds the spatial scale of parent-offspring competition (Giladi 2006). For trees, even a dispersal distance of 10 m may not remove a seed from parental influence. More generally, primary seed shadows are strongly related to plant size (Cousens *et al.* 2008), and dispersal by ants will have far less of an effect on ultimate seed shadows for trees, compared with small-statured plants.

Interestingly, only a small proportion (11.5%) of herbaceous euphorbs in Caatinga is myrmecochorous, despite their small stature. All these species are annuals, occurring in a vegetative state for only a few months each year (Reis *et al.* 2006, Silva *et al.* 2009). By contrast, the myrmecochorous herbs of the northern hemisphere (*e.g.*, species of *Anemone*, *Asarum*, *Carex*, *Corydalis*, *Trillium*, *Viola*) are mostly perennial (Beattie & Culver 1981). This suggests that myrmecochory is linked to perenniality, perhaps because short-lived plants cannot easily acquire the resources for elaiosome production.

CONCLUSION

We argue that myrmecochory rarely occurs in trees because ants do not offer distance dispersal benefits for tall plants. Further, we argue that the primary benefit of distance dispersal is avoidance of parental and sibling competition. This is consistent with a recent review demonstrating that dispersal distance is positively related to the canopy radius of myrmecochorous plants (Gómez & Espadaler 2013). A reduction in density dependent seed predation by rodents (Janzen 1970) is unlikely to be a factor, given that predation by rodents is often very low where myrmecochores occur, and major gradients in rodent predation occur at larger spatial scales than the few meters that typically apply to myrmecochory.

The distance dispersal of seeds transported by ants is driven by the density and the distribution of their nests (Andersen 1988a), their body size (Gómez & Espadaler 1998, Ness *et al.* 2004), and the distribution of seeds on the soil surface relative to nearby ant nests (Gómez & Espadaler 1998). Therefore, the local seed dispersal curve reflects varying characteristics of local ant communities (Gómez & Espadaler 1998, 2013). Anthropogenic disturbance can also strongly influence dispersal. For example, ant species responsible for long-distance dispersals in Caatinga are highly sensitive to disturbance, so distance dispersal decreases markedly with increasing disturbance (Leal *et al.* 2014a). In contrast, mean dispersal distance increases markedly following moderate disturbance (*e.g.*, fire events) in Australian tropical savannahs (Andersen & Morrison 1998, Parr *et al.* 2007). Thus, anthropogenic disturbance likely affects recruitment by myrmecochorous plants, and, in the longer term, vegetation composition and structure.

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LITERATURE CITED

ANDERSEN, A. N. 1988a. Dispersal distance as a benefit of myrmecochory. Oecologia 75: 507–511.

ANDERSEN, A. N. 1988b. Nest mound soil of the seed dispersing ant *Aphaenogaster longiceps* enhances seedling growth. Aust. J. Ecol. 13: 469–471.

ANDERSEN, A. N., AND S. MORRISON. 1998. Myrmecochory in Australia's seasonal tropics: effects of disturbance on distance dispersal. Aust. J. Ecol. 23: 483–491.

BEATTIE, A. J. 1985. The evolutionary ecology of ant-plant mutualisms, 1st edn. Cambridge University Press, Cambridge, MA, USA.

BEATTIE, A. J., AND D. C. CULVER. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. Ecology 62: 107–115.

BERG, R. Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. Aust. J. Bot. 62: 714–722.

BOND, W., AND P. SLINGSBY. 1983. Seed dispersal by ants in Cape shrublands and its evolutionary implications. S. Afr. J. Sci. 79: 231–233.

BONO, J. M., AND E. R. HEITHAUS. 2002. Sex ratios and the distribution of elaiosomes in colonies of the ant. Aphaenogaster. Rudis. Insectes Soc. 49: 320–325.

BOYD, R. S. 2001. Ecological benefits of myrmecochory for the endangered chaparral shrub *Fremontodendron decumbens* (Sterculiaceae). Am. J. Bot. 88: 234–241.

COUSENS, R. D., T. WIEGAND, AND M. S. TAGHIZADEH. 2008. Small-scale spatial structure within patterns of seed dispersal. Oecologia 158: 437–448.

CULVER, D. C., AND A. C. BEATTIE. 1978. Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. J. Ecol. 66: 53–72.

CULVER, D. C., AND A. C. BEATTIE. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in Colorado montane meadow. Ecology 64: 53–72.

GARRIDO, J. L., P. J. REY, X. CERDÁ, AND C. M. HERRERA. 2002. Geographical variation in diaspore traits of an ant-dispersed plant (*Helleborus foetidus*): are ant community composition and diaspore traits correlated? J. Ecol. 90: 446–455.

GILADI, I. 2006. Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos 112: 481–492.

GÓMEZ, C., AND X. ESPADALER. 1998. Myrmecochorous dispersal distances: a world survey. J. Biogeogr. 25: 573–580.

GÓMEZ, C., AND X. ESPADALER. 2013. An update of the world survey of myrmecochorous dispersal distances. Ecography 36: 1193–1201.

HANZAWA, F. M., A. J. BEATTIE, AND D. C. CULVER. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. Am. Nat. 131: 1–13.

HEITHAUS, E. R. 1981. Seed predation by rodents on three ant-dispersed plants. Ecology 62: 136–145.

HIGASHI, S., S. TSUYUZAKI, AND I. F. OHARA. 1989. Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). Oikos 54: 389–394.

HUGHES, L., M. DUNLOP, K. FRENCH, M. R. LEISHMAN, B. RICE, L. RODGERSON, AND M. WESTOBY. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. J. Ecol. 82: 933–950.

HUGHES, L., AND M. WESTOBY. 1992. Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. Ecology 73: 1285–1299.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104: 501–528.

LEAL, L. C., A. N. ANDERSEN, AND I. R. LEAL. 2014a. Anthropogenic disturbance reduces seed dispersal services for myrmecochorous plants in the Brazilian Caatinga. Oecologia 174: 173–181.

LEAL, L. C., M. C. LIMA-NETO, A. F. M. OLIVEIRA, A. N. ANDERSEN, AND I. R. LEAL. 2014b. Myrmecochores can target high-quality disperser ants: variation in elaiosome traits and ant preferences for myrmecochorous Euphorbiaceae in Brazilian Caatinga. Oecologia 174: 493–500.

LEAL, I. R., AND P. S. OLIVEIRA. 1998. Interactions between fungus-growing ants (Attini), fruits and seeds in cerrado vegetation in Southeast Brazil. Biotropica 30: 170–178.

LEAL, I. R., R. WIRTH, AND M. TABARELLI. 2007. Seed dispersal by ants in the semi-arid Caatinga of North-east Brazil. Ann. Bot. 99: 885–894.

LENGYEL, S., A. D. GOVE, A. M. LATIMER, J. D. MAJER, AND R. R. DUNN. 2009. Ants sow the seeds of global diversification in flowering plants. PLoS One 4(5): e5480.

LENGYEL, S., A. D. GOVE, A. M. LATIMER, J. D. MAJER, AND R. R. DUNN. 2010. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. Persp. Plant Ecol. Evol. Syst. 12: 43–55.

LÔBO, D., M. TABARELLI, AND I. R. LEAL. 2011. Realocation of *Croton sonderianus* (Euphorbiaceae) seeds by *Pheidole fallax* Mayr (Formicidae): a case of post-dispersal seed protection by ants. Neotrop. Entomol. 40: 440–444.

MILEWSKI, A. V., AND W. J. BOND. 1982. Convergence of myrmecochory in mediterranean Australia and South Africa. In R. C. Buckley (Ed.). Ant-plant interactions in Australia, pp. 89–98. Dr. W. Junk Publishers, Dordrecht, the Netherlands.

MORALES, M. A., AND E. R. HEITHAUS. 1998. Food from seed dispersal mutualism shifts sex ratios in colonies of the ant *Aphaenogaster rudis*. Ecology 79: 734–739.

NESS, J. H., J. L. BRONSTEIN, A. N. ANDERSEN, AND J. N. HOLLAND. 2004. Ant body size predicts dispersal distance of ant-adapted seeds: implications of small-ant invasions. Ecology 85: 1244–1250.

OHARA, M., AND S. HIGASHI. 1987. Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). J. Ecol. 75: 1091–1098.

OHKAWARA, K., S. HIGASHI, AND M. OHARA. 1996. Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne (Liliaceae). Oecologia 106: 500–506.

PARR, C. L., A. N. ANDERSEN, C. CHASTAGNOL, AND C. DUFFAUD. 2007. Savanna fires increase rate of myrmecochory and dispersal distance by ants. Oecologia 151: 33–41.

PASSOS, L., AND S. O. FERREIRA. 1996. Ant dispersal of *Croton priscus* (Euphorbiaceae) seeds in a tropical semideciduous forest in southeastern Brazil. Biotropica 28: 697–700.

PASSOS, L., AND P. S. OLIVEIRA. 2003. Interaction between ants, fruits and seeds in a restinga forest in southeastern Brazil. J. Trop. Ecol. 19: 261–270.

PENNINGTON, R. T., M. LAVIN, AND A. OLIVEIRA-FILHO. 2009. Woody plant diversity, evolution, and ecology in the tropics: perspectives from Seasonally Dry Tropical Forests. Annu. Rev. Ecol. Evol. Syst. 40: 437–457.

PIZO, M. A., AND P. S. OLIVEIRA. 2000. The use of fruits and seeds by ants in the Atlantic forestof southeast Brazil. Biotropica 32: 851–861.

PRADO, D. E. 2003. As caatingas da América do sul. In R. Leal, M. Tabarelli, and J. M. C. Silva (Eds.). Ecologia e conservação da caatinga I, pp. 3–74. Editora Universitária da UFPE, Recife, PE, Brazil.

R DEVELOPMENT CORE TEAM. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

REIS, A. M. S., E. L. ARAUJO, E. M. N. FERRAZ, AND A. N. MOURA. 2006. Inter-annual variations in the floristic and population structure of an herbaceous community of "caatinga" vegetation in Pernambuco. Brazil. Rev. Bras. Bot. 29: 497–508.

RIZZINI, C. T. 1979. Tratado de fitogeografia do Brasil: Aspectos ecológicos, sociológicos e florísticos. Âmbito Cultural Edições Ltda, Rio de Janeiro, RJ, Brazil.

Rodal, M. J. N., and A. L. Melo. 1996. Levantamento preliminar das espécies lenhosas da Caatinga de Pernambuco. In F. A. Araújo, H. D. V. Prendergast, and S. J. Mayo (Eds.). Anais do I Workshop Geral do programa Plantas do Nordeste, pp. 53–62. Associação Plantas do Nordeste, Recife, PE, Brazil.

Silva, K. A., E. L. Araujo, and E. M. N. Ferraz. 2009. Estudo florístico do componente herbáceo e relação com solos em áreas de caatinga do embasamento cristalino e bacia sedimentar, Petrolândia, PE. Brasil. Acta Bot. Bras. 23: 100–110.

Smith, B. H., P. D. Forman, and A. E. Boyd. 1989. Spatial patterns of seed dispersal and predation of 2 myrmecochorous forest herbs. Ecology 70: 1649–1656.

Thakur, H. A., and D. A. Patil. 2011. Taxonomic and phylogenetic assessment of the Euphorbiaceae: a review. J. Exp. Sci. 2: 37–46.

Westoby, M., K. French, L. Hugdes, B. Rice, and L. Rodgerson. 1991. Why do more plant species use ants for dispersal on infertile compared with fertile soils? Aust. J. Ecol. 16: 445–455.

Westoby, M., B. Rice, J. M. Shelley, D. Haig, and J. L. Kohen. 1982. Plant's use of ants for dispersal at West Head, NSW. *In* R. C. Buckley (Ed.). Ant-Plant Interactions in Australia, pp. 75–87. Junk Press, The Hague, the Netherlands.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall Inc., Upper Saddle River, NJ.