Journal of Mammalogy, 81(2):563–570, 2000

CONSUMPTION OF ARBUSCULAR MYCORRHIZAL FUNGI BY TERRESTRIAL AND ARBOREAL SMALL MAMMALS IN A PANAMANIAN CLOUD FOREST

SCOTT A. MANGAN AND GREGORY H. ADLER*

Department of Biology and Microbiology, University of Wisconsin, Oshkosh, WI 54901

Fecal pellets collected from 10 small-mammal species captured in a Panamanian cloud forest were examined for presence of spores of arbuscular mycorrhizal fungi. Fifty-two percent of the 94 fecal samples examined contained spores of ≥1 of 6 arbuscular mycorrhizal fungi species, including *Sclerocystis coremioides, Glomus fasciculatum, G. rubiforme, G. geosporum,* and 2 unidentified *Glomus* species. *G. fasciculatum* was the most frequently encountered species, occurring in 87% of the fecal samples that contained spores and occurring in diets of 7 small-mammal species occupying terrestrial and arboreal habitats. *Peromyscus mexicanus* and *Oryzomys devius* frequently consumed arbuscular mycorrhizal fungi and may be important spore dispersers in terrestrial habitats. Arbuscular mycorrhizal fungal spores also were common in diets of the primarily arboreal rodent *Reithrodontomys mexicanus,* suggesting a potentially important role of this species in the dispersal of arbuscular mycorrhizal fungal spores to epiphytes of Neotropical cloud forests.

Key words: arbuscular mycorrhizal fungi, cloud forest, mycophagy, Neotropics, Panama, rodents, spore dispersal

---

Many species of small mammals serve as seed predators and dispersers in tropical forests and therefore have been implicated as important participants in forest regeneration (Adler and Kestell 1998; Asquith et al. 1997; Forget and Milleron 1991). Small mammals also may contribute positively to tree seedling survival by dispersing spores of arbuscular mycorrhizal fungi (AMF) in tropical forests (Janos et al. 1995; Mangan and Adler 1999; Reddell et al. 1997). Tropical trees depend strongly on AMF for enhanced growth and survival (Janos 1980b; Siqueira et al. 1998). The improved uptake of scarce nutrients by plants hosting AMF may subsequently influence coexistence of plant species in the notoriously nutrient-poor soils of the tropics (Janos 1980a).

Like their terrestrial counterparts, plants that have evolved epiphytic strategies reach their highest diversity in Neotropical cloud forests (Gentry and Dodson 1987). Although many species of epiphytic plants can host mycorrhizal fungi, colonized individuals are less common and more patchily distributed than individuals of terrestrial species capable of hosting AMF (Lesica and Antibus 1990; Maffia et al. 1993; Michelsen 1993; Nadarajah and Nawawi 1993; Rabatin et al. 1993). Reduced availability of AMF inocula (e.g., spores, fungal hyphae, and colonized roots) at arboreal sites has been proposed as an explanation for less frequent AMF colonization in epiphytic plants (Lesica and Antibus 1990; Maffia et al. 1993; Michelsen 1993). Epiphytes that host AMF reside in spatially isolated patches of habitat that contain sufficient AMF inocula to support colonization. Thus, such sites capable of supporting colonized epiphytes probably are established through the dispersal of AMF inocula from the forest floor to the canopy.

* *Correspondent: adler@uwosh.edu*

In terrestrial plant communities, AMF can be dispersed through the spread of fungal hyphae in the soil (Harinikumar and Bagyaraj 1995; Powell 1979), by root-to-root contact with colonized hosts (Alexander et al. 1992), and by the movement of AMF spores via wind erosion of soil in arid regions (Allen et al. 1989). These dispersal mechanisms, however, are unlikely to account for the introduction of AMF to arboreal sites because canopies are disconnected from terrestrial root networks, and wind dispersal of spores is uncommon in tropical forests. The most probable mechanism of AMF introduction to the canopy is dispersal of fungal spores via animal vectors (Janos 1993). Although soil invertebrates have been shown to disperse AMF spores incidentally (McIlveen and Cole 1976; Reddell and Spain 1991), these organisms may not be as important to long-distance dispersal as would larger animals that actively consume mycorrhizal fungi. Many terrestrial species of small mammals of lowland tropical regions consume AMF sporocarps and pass large quantities of spores in their feces (Emmons 1982; Janos et al. 1995; Mangan and Adler 1999). Because many spores are viable after passing through digestive tracts of rodents (Reddell et al. 1997; Rothwell and Holt 1978; Trappe and Maser 1976), small mammals have been implicated as potentially important AMF dispersers of both tropical and temperate regions.

In Neotropical cloud forests, several species of small mammals use both the forest floor and the canopy (Emmons and Feer 1997). Because epiphytes host the same AMF species as found in soils of the forest floor (Maffia et al. 1993), small mammals that consume sporocarps in terrestrial soil and subsequently defecate spores at arboreal sites may serve as important AMF dispersers to epiphytes. Unfortunately, little is known about the dietary habits of most small mammals of Neotropical cloud forests (Emmons and Feer 1997).

We investigated AMF consumption by small mammals in a Panamanian cloud forest. Feces collected from small mammals captured both on the ground and in trees were examined for presence of AMF spores to identify potentially important dispersers of AMF spores to terrestrial and arboreal habitats.

Materials and Methods

Study site.—The study was conducted in a lower montane wet forest at 1,100 m elevation in the Central Cordillera of Chiriquí Province, western Panamá. These mountains comprise the Fortuna drainage basin, in which rainwater flows into a man-made lake created for producing hydroelectric power. Because the surrounding vegetation buffers against erosion, this region is protected rigidly by the Instituto de Recursos Hidraulicos y Energeticos and remains mostly as primary forest. The study site was near a former Instituto de Recursos Hidraulicos y Energeticos facility used now by the Smithsonian Tropical Research Institute as their Fortuna field station.

Annual rainfall was about 4,000 mm at the study location, with most falling from May through December (Cavelier et al. 1997). Average canopy height at the study site was 18.5 m (G. H. Adler, in litt.), and the canopy and lower strata supported abundant epiphytes (Cavelier et al. 1996).

Sampling procedures.—During July 1998, we established 2 sampling transects to census small mammals within mostly primary cloud forest. Both transects contained 55 sampling stations spaced 20 m apart. We placed live traps both on the ground and in trees to determine the proportion of captures at each habitat type (terrestrial versus arboreal) for each small-mammal species. At each station, 1 Tomahawk live trap (40.5 by 12.6 by 12.7 cm) and 1 Sherman live trap (22.9 by 8.9 by 7.6 cm) were placed on the forest floor within 2 m of each other. Single Tomahawk and Sherman traps also were placed in trees and lianas at each station. Arboreal traps were placed within 4 m of the ground, which was deemed sufficient to sample mammals moving between the forest floor and canopy. Traps were baited with a mixture of sweet potato, peanut butter, and bird seed and were set for 10 consecutive nights and checked each morning. All captured mammals were identified and weighed, and sex and age were determined (based on pelage char-

acteristics). Each individual was marked uniquely by toeclipping (strictly terrestrial species) or earnotching (arboreal species) for permanent identification and was released at the station of capture.

Fecal pellets from each captured mammal were collected from the bottom of the trap and placed into a vial containing 70% ethanol. We selected dark, firm pellets to avoid samples contaminated by bait. Pellets were collected only upon 1st capture of an individual.

In the laboratory, 2–5 fecal pellets (depending on availability) from each individual were processed together. Composite samples (hereinafter referred to as single samples) were air dried, weighed to the nearest 0.001 g, and placed in a 9-cm gridded Petri dish containing distilled water. Each sample was lightly crushed into a fine debris, and contents were swirled to obtain a thin, even distribution. The entire Petri dish was scanned under 40× magnification, and all AMF spores or whole sporocarps were grouped by morphotype and counted. For each sample, spore density was computed by dividing total number of spores or sporocarps (separately for each AMF species) by the dried weight of the composite sample. All samples were standardized to 0.025 g. Representative spores of each morphotype were mounted on slides and identified to species under higher magnification. Permanent slide vouchers for all AMF species were deposited in the herbarium at the University of Wisconsin–Oshkosh and are available upon request.

Statistical analysis.—We tallied number of individuals captured for each small-mammal species and total number of captures in ground and arboreal traps. Proportion of captures on the ground and in trees was used as a relative measure of habitat use. For small-mammal species that had ≥20 total captures, terrestrial and arboreal habitat use was compared by constructing linear models of repeated categorical data because multiple captures of some individuals were included in the analysis (Kleinbaum and Kupper 1978).

Fungal consumption was assessed by tabulating total number of fecal samples that contained AMF spores for each species of small mammal. Only small-mammal species with >15 fecal samples were used in this analysis. Total number of individuals for which fecal samples were examined differed from the total number captured because we were unable to collect samples from all individuals. The proportion of samples containing spores (all AMF species combined) was compared among the different small-mammal species by chi-square analysis. Chi-square analysis also was used to compare the proportion of samples containing AMF spores (all species combined) between sexes separately for each small-mammal species. For each small-mammal species, mean densities of spores of common AMF species were log transformed, and means were compared among small-mammal species by analysis of variance (ANOVA) for unbalanced group design (SAS Institute Inc. 1993).

RESULTS

Small-mammal species and habitat use.—We recorded 290 captures of 169 small mammals, including 151 individuals of 8 species of rodents and 18 individuals of 3 species of marsupials (Table 1). *Reithrodontomys mexicanus, Peromyscus mexicanus,* and *Oryzomys devius* were the most frequently captured species, comprising 67% of the total number of individuals. *Oligoryzomys vegetus* and *Oryzomys alfaroi* represented 17% of the total number of individuals captured. The 3 remaining rodent species, *Heteromys desmarestianus, Nyctomys sumichrasti,* and *Tylomys watsoni,* and the 3 marsupial species, *Didelphis marsupialis, Marmosa mexicana,* and *Marmosops invictus,* were encountered rarely, with captures of ≤8 individuals/species (Table 1).

Five species of rodents had sufficient sample sizes for statistical analysis of habitat use. Terrestrial and arboreal captures differed among the 5 species ($\chi^2 = 329.92$, $d.f. = 4$, $P = 0.0001$; Table 1). *R. mexicanus* was captured more frequently in trees (86% of captures), whereas *P. mexicanus* (91%), *O. devius* (88%), *O. alfaroi* (100%), and *O. vegetus* (82%) were captured more frequently on the ground. Although our data suggest that *R. mexicanus* is largely arboreal, some individuals also were captured on the ground. Similarly, individuals of *P. mexicanus, O. devius,* and *O. vegetus* (predominately captured on the ground) also were captured in arboreal traps. *O. alfaroi*

TABLE 1.—Total number of individuals per small-mammal species and total number of captures in traps set on the ground and in trees. Percentage of total captures by terrestrial and arboreal traps is in parentheses.

Mammal	Total no. individuals	Total no. captures	
		Terrestrial	Arboreal
Marsupials			
Didelphis marsupialis	8	12 (0.71)	5 (0.29)
Marmosops invictus	8	0	10 (1.00)
Marmosa mexicana	2	0	4 (1.00)
Rodents			
Heteromys desmarestianus	5	5 (1.00)	0
Nyctomys sumichrasti	5	0	11 (1.00)
Oligoryzomys vegetus	17	19 (0.82)	4 (0.18)
Oryzomys alfaroi	11	21 (1.00)	0
Oryzomys devius	32	71 (0.88)	10 (0.12)
Peromyscus mexicanus	39	60 (0.91)	6 (0.09)
Reithrodontomys mexicanus	40	7 (0.14)	43 (0.86)
Tylomys watsoni	2	0	2 (1.00)

was the only commonly recorded species that was captured exclusively on the ground (Table 1). Of the less frequently captured rodents, *N. sumichrasti* and *T. watsoni* were captured only in trees, and *H. desmarestianus* was captured exclusively on the forest floor.

All 3 species of marsupials occurred above ground (Table 1). All captures of *M. invictus* and *M. mexicana* were in tree traps. Although *D. marsupialis* also was captured in arboreal traps, 71% of the captures for this species were on the ground (Table 1).

Occurrence of arbuscular mycorrhizal fungi spores.—Fecal samples were collected from all species except *T. watsoni*. Fifty-two percent of the 94 fecal samples contained AMF spores, with spores being present in diets of 7 of the remaining 10 species of small mammals (Table 2). We identified spores of 6 species from 2 AMF genera, *Glomus* and *Sclerocystis*. *G. fasci-*

TABLE 2.—Number of fecal samples containing arbuscular mycorrhizal fungi (AMF) spores for each small-mammal species. Cumulative number of AMF taxa encountered in samples of each species of small mammal also is shown.

Mammal	*n*	No. (%) samples with AMF spores	No. AMF taxa
Marsupials			
Didelphis marsupialis	4	0	0
Marmosops invictus	5	2 (0.40)	3
Marmosa mexicana	2	1 (0.50)	1
Rodents			
Heteromys desmarestianus	4	2 (0.50)	1
Nyctomys sumichrasti	3	0	0
Oligoryzomys vegetus	8	1 (0.13)	1
Oryzomys alfaroi	2	0	0
Oryzomys devius	18	12 (0.67)	2
Peromyscus mexicanus	22	19 (0.86)	6
Reithrodontomys mexicanus	26	12 (0.46)	2

culatum was by far the most frequently consumed fungal species. This species was found in 87% of the fecal samples that contained spores and in samples of all 7 mycophagous small mammals (Table 2). Spores of *G. fasciculatum* are produced in tight, unorganized sporocarps (Gerdemann and Trappe 1974; Walker and Koske 1987), which apparently are consumed by many small mammals of this region.

Two AMF species that produce highly organized sporocarps (*Sclerocystis coremioides* and *G. rubiforme*—Almeida and Schenck 1990) were encountered less frequently. Intact sporocarps of *S. coremioides* were found in 18.4% of fecal samples containing AMF and from 2 species of small mammals, *P. mexicanus* and *O. devius.* Both spores and intact sporocarps of *G. rubiforme* were encountered in 10.2% of fecal samples containing AMF; however, this species was found only in fecal samples of *P. mexicanus. G. geosporum* was found in only 3 fecal samples, and 2 unidentified species of *Glomus* each were found in only 2 fecal samples.

Of the 7 mammal species that deposited AMF spores, 4 occupied predominately terrestrial habitat, and 3 were captured more commonly in trees (Table 2). We were able to include *P. mexicanus, O. devius,* and *R. mexicanus* for statistical analysis of spore occurrence. The proportion of samples containing spores did not differ between sexes for any of the rodent species (*P. mexicanus*: $\chi^2 = 0.22$, *d.f.* = 1, $P = 0.637$; *O. devius*: $\chi^2 = 0.47$, *d.f.* = 1, $P = 0.494$; *R. mexicanus*: $\chi^2 = 0.10$, *d.f.* = 1, $P = 0.756$). Although individuals of those species commonly passed AMF spores, the number of samples containing spores significantly differed among the 3 species ($\chi^2 = 8.51$, *d.f.* = 2, $P = 0.014$); spores were most frequent in pellets collected from *P. mexicanus* (Fig. 1). Furthermore, spores from all AMF species encountered in our study occurred in samples collected from *P. mexicanus,* with single fecal samples from several individuals containing up to 3 AMF species.

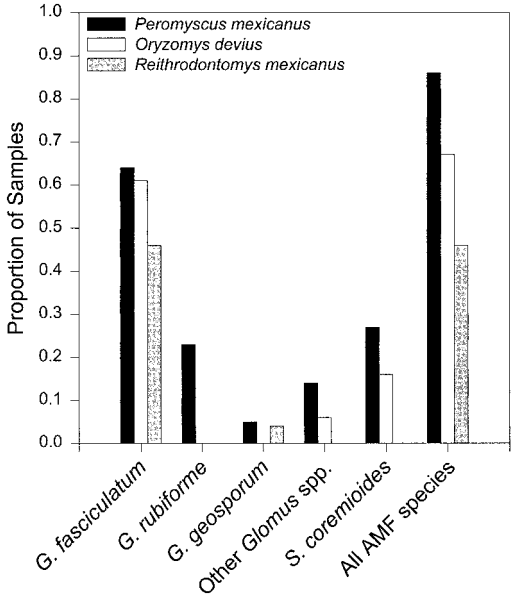

FIG. 1.—Proportion of fecal samples containing each arbuscular mycorrhizal fungus (AMF) taxon for 3 commonly captured rodent species in a Neotropical cloud forest.

Glomus fasciculatum was the dominant AMF species encountered in fecal samples collected from the 3 rodent species (Fig. 1). For fecal samples that contained *G. fasciculatum,* mean log-transformed number of spores per 0.025 g of fecal material did not differ significantly among rodent species (*O. devius*: 2.599 ± 0.736 *SD*; *P. mexicanus*: 2.136 ± 0.634 *SD*; *R. mexicanus*: 2.226 ± 0.640 *SD*; $F = 1.606$; *d.f.* = 2, 34; $P = 0.216$).

DISCUSSION

Consumption of AMF species apparently is widespread among small mammals of this montane fauna. Seven of the 10 species examined contained AMF spores or whole sporocarps in their feces. Several authors have suggested that small mammals actively (versus incidentally) consume AMF species only of genera that produce their spores in clusters or organized sporocarps (Gerdemann and Trappe 1974; Janos et al. 1995). Despite the co-occurrence of nonsporocarpic AMF species in the soil, only

TABLE 3.—Number of samples in which the most common arbuscular mycorrhizal fungi species occurred, including each respective mean number of single spores or intact sporocarps per 0.025 g of fecal material.

Fungus	*n*	$\bar{X}$	*SE*	Range
Glomus fasciculatum (spores)	43	493.1	112.3	13–2,775
G. rubiforme (spores)	5	52.4	23.4	5–165
G. rubiforme (sporocarps)	5	5.2	2.5	1–15
Sclerocystis coremioides (sporocarps)	10	9.1	3.9	1–40

spores from *Sclerocystis* and several sporocarpic species of *Glomus* commonly occur in stomach contents or fecal pellets of small mammals (Fogel and Trappe 1978; Janos et al. 1995; Maser et al. 1978; McGee and Baczocha 1994). The ubiquity of spores of *G. fasciculatum* (Table 3) and frequent occurrence of spores and intact sporocarps of 2 highly organized sporocarpic species (*G. rubiformes* and *S. coremioides*) in fecal pellets collected at our study site corroborate these previous findings. We therefore suggest that many small-mammal species in cloud forests of Panamá actively seek and include at least some species of AMF in their diets. Because consumption of AMF sporocarps by small mammals probably is active, dispersal of spores of these AMF species undoubtedly is more frequent than if spores were consumed only incidentally.

Investigations of small-mammal mycophagy generally have focused on terrestrial species. However, we identified mycophagy by both terrestrial and arboreal species of small mammals. The common occurrence of AMF spores in the pellets of *R. mexicanus* is of particular interest. Not only do trapping records indicate that this small rodent is primarily arboreal, individuals frequently were observed to climb high into the canopy following their release. Because 10 of the 12 fecal samples that contained spores were collected from tree traps and mean densities of *G. fasciculatum* spores found in scats of *R. mexicanus* did not differ from densities in scats of other mycophagous species, *R. mexicanus* may be important in moving spores of this AMF species to the canopy and lower arboreal strata.

Arboreal marsupials such as *M. invictus* and *M. mexicana* may play a role similar to that of *R. mexicanus.* Although only a few samples were examined, 2 of the 5 fecal samples collected from *M. invictus* in tree traps contained spores from 3 AMF species. Presumably, AMF sporulating in terrestrial soils provide a food source for these arboreal mammals. However, the lack of captures of either marsupial species on the ground suggests a need for studies assessing sporocarp densities in canopy soils because these soils also may provide fruiting bodies for mycophagous mammals. In such case, spores would not only move vertically from the forest floor to the canopy and lower strata but also would move horizontally among trees.

Because of their high abundance and frequent consumption of AMF, *O. devius* and *P. mexicanus* undoubtedly are important spore dispersers in terrestrial habitats. Moreover, because individuals of both species were captured in trees, these rodents also may move AMF spores to at least lower arboreal sites. Mycophagy apparently is common in both genera of small mammals; other species of *Peromyscus* (Maser and Maser 1987) and *Oryzomys* (Janos et al. 1995) have been reported to consume AMF. In our study, *P. mexicanus* was the most avid consumer of AMF, with 86% of the samples containing spores from 6 different fungal species. Most fecal pellets collected from individuals of *P. mexicanus* also contained >1 AMF species. Because *P. mexicanus* also is frugivorous and is known to

scatterhoard seeds (Emmons and Feer 1997), this rodent may play an ecological role similar to that of the tropical lowland rodent *Proechimys semispinosus.* Like *P. mexicanus, P. semispinosus* actively consumes AMF (Mangan and Adler 1999) and serves as an important seed predator and disperser in lowland forests (Adler and Kestell 1998; Hoch and Adler 1997). Studies of potential interactions between mycophagy and frugivory by these rodents would aid in understanding implications of spore and seed dispersal on the ecology of tropical forests.

Long-distance movement of spores facilitated by small mammals is important in reintroducing AMF to soils after large-scale disturbances (Allen 1987) and probably to inoculum-poor microsites within intact forests (see Janos 1992). Because of the discontinuity of suitable substrates in forest canopies, AMF dispersal via root-to-root contact is limited because expansive root networks cannot be established (Janos 1993). Therefore, introduction of spores to newly formed arboreal sites (e.g., branches) is necessary for AMF colonization of epiphytic plants. In documenting mycophagy by several species of scansorial and arboreal small mammals (in particular *R. mexicanus*), we have identified at least 1 probable mechanism for the movement of AMF spores to canopies of Neotropical cloud forests.

Acknowledgments

We thank S. P. Bentivenga for assisting in spore identification. S. P. Bentivenga, J. M. Trappe, and an anonymous reviewer provided helpful comments on an earlier draft of this manuscript. We are also grateful to Administrativa Nacional del Ambiente and Instituto de Recursos Hidraulicos y Energeticos for providing permits to conduct this study and the Smithsonian Tropical Research Institute for the use of their facility. This study was supported in part by grants from the Zoological Society of Milwaukee County to S. A. Mangan and from the United States National Science Foundation (grant DEB-96-28943) to G. H. Adler.

Literature Cited

Adler, G. H., and D. W. Kestell. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). Biotropica 30:677–681.

Alexander, I., N. Ahmad, and L. S. See. 1992. The role of mycorrhizas in the regeneration of some Malaysian forest trees. Philosophical Transactions of the Royal Society of London 335:379–388.

Allen, M. F. 1987. Re-establishment of mycorrhizas on Mount St. Helens: migration vectors. Transactions of the British Mycological Society 88:413–417.

Allen, M. F., L. E. Hipps, and G. L. Wooldridge. 1989. Wind dispersal and subsequent establishment of VA mycorrhizal fungi across a successional arid landscape. Landscape Ecology 2:165–171.

Almeida, R. T., and N. C. Schenck. 1990. A revision of the genus *Sclerocystis* (Glomaceae, Glomales). Mycologia 82:703–714.

Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control seedling recruitment in Neotropical forests? Evidence from Panamá. Ecology 78:941–946.

Cavelier, J., M. Jaramillo, D. Solis, and D. de Leon. 1997. Water balance and nutrient inputs in bulk precipitation in tropical montane cloud forest in Panama. Journal of Hydrology 193:83–96.

Cavelier, J., D. Solis, and M. A. Jaramillo. 1996. Fog interception in montane forests across the Central Cordillera of Panama. Journal of Tropical Ecology 12:357–369.

Emmons, L. H. 1982. Ecology of *Proechimys* (Rodentia, Echimyidae) in south-eastern Peru. Tropical Ecology 23:280–290.

Emmons, L. H., and F. Feer. 1997. Neotropical rainforest mammals: a field guide. 2nd ed. The University of Chicago Press, Chicago, Illinois.

Fogel, R., and J. M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science 52:1–29.

Forget, P. M., and T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in Panamá. Oecologia (Berlin) 87:596–599.

Gentry, A. H., and C. H. Dodson. 1987. Diversity and biogeography of Neotropical vascular epiphytes. Annals of the Missouri Botanical Garden 74:205–233.

Gerdemann, J. W., and J. M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. Mycologia Memoirs 5:1–76.

Harinikumar, K. M., and D. J. Bagyaraj. 1995. Spread of vesicular arbuscular mycorrhizal fungal hyphae in soil. Microbiological Research 150:77–80.

Hoch, G. A., and G. H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). Journal of Tropical Ecology 13:51–58.

Janos, D. P. 1980a. Mycorrhizae influence tropical succession. Biotropica (Supplement) 12:56–64.

Janos, D. P. 1980b. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151–162.

Janos, D. P. 1992. Heterogeneity and scale in tropical

vesicular-arbuscular mycorrhiza formation. Pp. 276–282 in Mycorrhizas in ecosystems (D. J. Read, D. H. Lewis, A. H. Fitter, and I. J. Alexander, eds.). CAB International, Wallingford, United Kingdom.

JANOS, D. P. 1993. Vesicular-arbuscular mycorrhizae of epiphytes. Mycorrhiza 4:1–4.

JANOS, D. P., C. T. SAHLEY, AND L. H. EMMONS. 1995. Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru. Ecology 76:1852–1858.

KLEINBAUM, D. G., AND L. L. KUPPER. 1978. Applied regression analysis and other multivariable methods. Duxbury Press, North Scituate, Massachusetts.

LESICA, P., AND R. K. ANTIBUS. 1990. The occurrence of mycorrhizae in vascular epiphytes of two Costa Rican rain forests. Biotropica 22:250–258.

MAFFIA, B., N. M. NADKARNI, AND D. P. JANOS. 1993. Vesicular-arbuscular mycorrhizae of epiphytic and terrestrial Piperaceae under field and greenhouse conditions. Mycorrhiza 4:5–9.

MANGAN, S. A., AND G. H. ADLER. 1999. Consumption of arbuscular mycorrhizal fungi by spiny rats (*Proechimys semispinosus*) in eight isolated populations. Journal of Tropical Ecology 15:779–790.

MASER, C., AND Z. MASER. 1987. Notes on mycophagy in four species of mice in the genus *Peromyscus.* The Great Basin Naturalist 47:308–313.

MASER, C., J. M. TRAPPE, AND R. A. NUSSBAUM. 1978. Fungal–small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59: 799–809.

MCGEE, P. A., AND N. BACZOCHA. 1994. Sporocarpic Endogonales and Glomales in the scats of *Rattus* and *Perameles.* Mycological Research 98:246–249.

MCILVEEN, W. D., AND H. COLE. 1976. Spore dispersal of Endogonaceae by worms, ants, wasps, and birds. Canadian Journal of Botany 54:1486–1489.

MICHELSEN, A. 1993. The mycorrhizal status of vascular epiphytes in Bale Mountains National Park, Ethiopia. Mycorrhiza 4:11–15.

NADARAJAH, P., AND A. NAWAWI. 1993. Mycorrhizal status of epiphytes in Malaysian oil palm plantations. Mycorrhiza 4:21–25.

POWELL, C. L. 1979. Spread of mycorrhizal fungi through soil. New Zealand Journal of Agricultural Research 22:335–339.

RABATIN, S. C., B. R. STINNER, AND M. G. PAOLETTI. 1993. Vesicular-arbuscular mycorrhizal fungi, particularly *Glomus tenue,* in Venezuelan bromeliad epiphytes. Mycorrhiza 4:17–20.

REDDELL, P., AND A. V. SPAIN. 1991. Earthworms as vectors of viable propagules of mycorrhizal fungi. Soil Biology and Biochemistry 23:767–774.

REDDELL, P., A. V. SPAIN, AND M. HOPKINS. 1997. Dispersal of spores of mycorrhizal fungi in scats of native mammals in tropical forests of northeastern Australia. Biotropica 29:184–192.

ROTHWELL, F. M., AND C. HOLT. 1978. Vesicular-arbuscular mycorrhizae established with *Glomus fasciculatus* spores isolated from the feces of cricetine mice. United States Forest Service Northeastern Forest Experiment Station Note NE-259:1–4.

SAS INSTITUTE. 1993. SAS/STAT user's guide. Version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.

SIQUEIRA, J. O., M. A. C. CARNEIRO, N. CURI, S. C. S. ROSADO, AND A. C. DAVIDE. 1998. Mycorrhizal colonization and mycotrophic growth of native woody species as related to successional groups in Southeastern Brazil. Forest Ecology and Management 107:241–252.

TRAPPE, J. M., AND C. MASER. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia 68:433–436.

WALKER, C., AND R. E. KOSKE. 1987. Taxonomic concepts in the Endogonaceae. IV. *Glomus fasciculatum* redescribed. Mycotaxon 30:253–262.

Submitted 25 February 1999. Accepted 9 September 1999.

Associate Editor was Renn Tumlison.