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RODENT DISPERSAL OF VESICULAR–ARBUSCULAR MYCORRHIZAL FUNGI IN AMAZONIAN PERU¹

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Abstract. We quantitatively assessed rodent dispersal of vesicular–arbuscular mycorrhizal fungi in a lowland tropical rain forest. We examined fecal pellets from seven rodent species of the genera *Proechimys*, *Oryzomys*, and *Mesomys* trapped each month from August 1983 through July 1984 at the Cocha Cashu field station in Manu National Park, Peru.

We found sporocarps of *Sclerocystis coremioides* and spores of four *Glomus* species in 69.3% of fecal samples, with 37.5% of samples containing 2–4 fungus species. There were median numbers of 8.6 *S. coremioides* sporocarps and 712 *Glomus* spores/0.1 g feces. *S. coremioides* and all *Glomus* species comprised up to 4.1 and 5.4% of fecal mass, respectively. We did not detect differences in fungus consumption by rodent species or sex, but did find significant differences between rodent genera. More than 60% of *Proechimys* samples contained glomalean fungi in contrast to ≈37% of *Oryzomys* samples. Occurrence of the two fungus genera in feces differed seasonally but was generally congruent between *Proechimys* and *Oryzomys*. *Glomus* presence in feces is significantly positively associated with the dry season. Both rodent genera together annually pass 2.96×10^5 *S. coremioides* sporocarps and 7.30×10^7 *Glomus* spores/ha at Cocha Cashu. We concluded that *Proechimys* and *Oryzomys* are likely to be important agents of vesicular–arbuscular mycorrhizal fungus spore dispersal.

Key words: *Echimyidae*; *Glomus*; *Muridae*; Peru; rodents; *Sclerocystis*; spore dispersal; tropical forest; vesicular–arbuscular mycorrhizal fungi.

INTRODUCTION

The absorptive roots of most plants associate mutually with zygomycetous fungi to form vesicular–arbuscular mycorrhizae (VAM) (Trappe 1987). VAM enhance uptake of mineral nutrients, especially those of low mobility in soil, such as phosphorus (Allen 1991). Because tropical rain forest soils often have limited available phosphorus (Vitousek 1984), VAM can increase plant growth and markedly improve survival (e.g., Janos 1980a). Therefore, if VAM form, they are likely to affect plant competition, influencing succession, community composition, and species diversity (e.g., Janos 1980b, 1983, 1985, Connell and Lowman 1989). Formation of VAM is dependent upon the availability of inoculum, of which one form is spores (Janos 1992).

Despite the predominance of VAM in tropical forests (Janos 1983, 1987), little is known about dispersal of VAM fungus spores. VAM fungi all belong to the order Glomales and produce either sporocarps, compact aggregations of spores, or single spores near roots (Morton 1988). Glomalean spores are among the largest of those of any fungi, with single spore diameters typically in the 50–250 μm range (Morton 1988). Because of their relatively large size, VAM spores are much

less efficient aerial disseminators than spores of other fungi (Morton 1988).

Evidence suggests that sporocarpic VAM fungi are adapted for dispersal by rodents. Spores of sporocarpic glomalean species are commonly ingested by rodents in the temperate zones (e.g., Maser et al. 1978, McGee and Baczocha 1994). Several authors have demonstrated that *Glomus* spores pass viably through the guts of small mammals (e.g., Trappe and Maser 1976, Warner et al. 1987) with germination rates of 30–75%. Emmons (1982) first reported *Glomus* spores in the caeca and feces of tropical rodents (*Proechimys*; *Echimyidae*), but the importance of this phenomenon in the tropics has not been determined.

The purpose of this investigation was to quantitatively assess the importance of rodents as dispersers of glomalean fungi in a lowland tropical rain forest. We determined the frequency, diversity, and abundance of propagules of these fungi in fecal samples from the widespread, common Neotropical rodent genera *Proechimys* (“spiny rats”), and *Oryzomys* (*Muridae*, “rice rats”).

METHODS

Study site, rodent species, and sample collection

The study site is located at Cocha Cashu field station in Manu National Park, Madre de Dios Department,

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Peru (11°51' S, 71°19' W; ≈400 m elevation). With 208 cm total annual precipitation and a distinct dry season from May through September (Fig. 3A), Cocha Cashu is classified as "tropical moist forest" in the Holdridge system (Terborgh 1983). The site is fully described by Terborgh (1983).

Fecal samples were collected from adults of seven rodent species, *Proechimys brevicauda* ($n = 7$), *P. simonsi* ($n = 11$), *P. steerei* ($n = 22$), *Mesomys hispidus* ($n = 1$), *Oryzomys capito* ($n = 40$), *O. nitidus* ($n = 6$), and *O. macconnelli* ($n = 1$). *Proechimys* species are large (150–550 g), completely terrestrial rats that often dominate the small-mammal biomass of Neotropical rain forests with 1–4 species occurring sympatrically (Emmons 1982, Guillotin 1982). They occur in both primary and disturbed forests, plantations and gardens, but not treeless areas such as pastures. *Oryzomys* are small rats (60–80 g) that are ubiquitous in Neotropical rain forests (Emmons and Feer 1990). *O. capito* is the dominant murid rat in evergreen rain forests, *O. nitidus* is rare in moist forest but dominates dry, deciduous forest, and *O. macconnelli* is a primary forest specialist of dense thickets. *M. hispidus* (130–220 g) is a generally uncommon arboreal rat of Amazonian rain forests, which favors dense, vine-filled habitats (Emmons and Feer 1990).

Rodents were trapped opportunistically in 41 × 13 × 13 cm collapsible live traps (National Live Trap Corp.) baited with banana for 4–5 d each month, usually within the first 2 wk of each month, from August 1983 through July 1984. Dark fecal pellets produced soon after capture were preferentially collected and placed into vials of 70% ETOH or FAA (formalin, acetic acid, alcohol) to prevent fungus growth. White pellets that included trap bait were discarded. Although samples were collected from different individuals within a month, in different months some individuals were recaptured. Fewer than one-quarter (23.9%) of fecal samples in this study, however, are from previously sampled individuals.

Sample analysis

Prior to examination, fecal pellets were air-dried to constant mass in the laboratory. Sample air-dry mass ranged from 0.005 to 0.327 g ($n = 88$, 0.121 ± 0.073 g, $\bar{X} \pm 1$ SD). After weighing, pellets were soaked in tap water to soften them and were manually teased apart with dissecting needles under a stereomicroscope at 15–45× magnification. Fungus species were differentiated by conventional taxonomic criteria (Morton 1988, Schenck and Pérez 1990).

All intact sporocarps were counted from each sample. We estimated the sizes of sporocarp fragments and included fractional sporocarps in totals. Loose spores were examined by compound microscopy.

In order to estimate the number of spores of each *Glomus* species per sample, feces were teased apart, stirred in 350 mL water until they were disaggregated,

and collected on a gridded 9 cm diameter Whatman Number 4 filter paper in a Buchner funnel. A relatively uniform, monolayered distribution of particles across the filter paper usually resulted. All spores of each fungus in 1-cm squares haphazardly located in each of four quadrants were counted at 60–75× and multiplied by one-fourth the paper area to estimate the sample total.

We made semi-permanent reference slides of all fungus species by mounting spores in polyvinylalcohol-lactic acid-glycerol (PVLG) (Koske and Tessier 1983). Nomenclature follows Morton and Benny (1990) and Schenck and Pérez (1990).

Statistical analysis

We tabulated the occurrence of fungus genera by month, rodent sex, rodent genus, and rodent species, and tested for association with a *G* statistic (Sokal and Rohlf 1981) using SYSTAT version 5.01 (Wilkinson 1990). If expected cell frequencies were 5% or less, we used Fisher exact probabilities for 2 × 2 tables. We computed Pearson product-moment correlation coefficients among: arcsine-transformed frequencies of occurrence (presence vs. absence) of fungus genera in fecal samples, monthly total precipitation (September 1976 through August 1977 as reported by Terborgh [1983], and separately, August 1983 through July 1984, the period of this study [L. H. Emmons, unpublished data]), monthly total mass of fruit fall per hectare in forest (Terborgh 1983), and monthly midpoint seed production (in kilojoules per hectare per day, estimated from Fig. 17.2 in Janson and Emmons 1990). We used Bonferroni probabilities to assess the significance of multiple a posteriori correlations.

RESULTS

Occurrence of fungi

More than two-thirds of the fecal samples that we examined (69.3%) contained sporocarps or spores of fungi belonging to the Glomineae (see Morton and Benny 1990). We found six species in all: one species of *Sclerocystis* (Berk. & Broome) Almeida & Schenck (Glomaceae), four of *Glomus* Tulasne & Tulasne (Glomaceae), and, in just one sample, only three spores of one *Entrophospora* Ames & Schneider (Acaulosporaceae). We encountered several types of spore-like objects without hyphal attachments or attachment scars and did not count them as spores. We did not observe spores of Basidiomycetes, but we did not search for them. Thirty-three samples (37.5%) contained more than one fungus species in the Suborder Glomineae to a maximum of four (Fig. 1). Presence of *Sclerocystis* was not significantly associated with presence of all *Glomus* species ($n = 88$, $G = 1.598$, $P = 0.206$). No single *Glomus* species presence in feces was significantly associated with that of any other.

We recovered many whole sporocarps of *Sclerocystis*

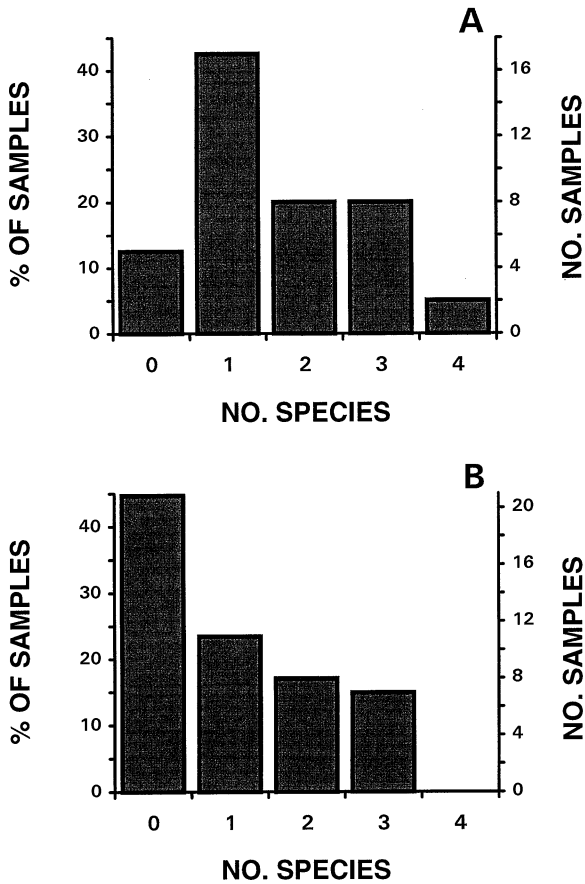


FIG. 1. Frequency of occurrence of species of Glomineae (Glomales, Zygomycetes) in fecal samples from Peruvian Amazonian rodents of the genera *Proechimys* (A, $n = 40$) and *Oryzomys* (B, $n = 47$). Abscissa shows number of species per sample.

coremioides Berk. & Broome, although some sporocarp fragments in feces appeared to have been cleanly sliced by rodents. Out of 42 samples that contained *S. coremioides*, 45.2% had >11 sporocarps/0.1 g feces (Fig. 2A). There were, as a median number, 8.6 sporocarps/0.1 g feces, which is equal to 0.45% of fecal mass (mean sporocarp mass of 5.25×10^{-5} g). The maximum number of intact sporocarps that we found in a 0.2077-g sample was 169, which comprised 4.1% of the feces by mass.

Among *Glomus* species, the most frequent, “*Glomus* species A,” is similar to *G. aggregatum* Schenck & Smith emend. Koske, but is likely an undescribed species. *G. macrocarpum* Tulasne & Tulasne was second in frequency (Table 1). We occasionally found clusters of 5–30 spores of *Glomus* species A and *G. macrocarpum*. *G. geosporum* (Nicolson & Gerdemann) Walker and *G. microcarpum* Tulasne & Tulasne, are the largest and smallest species respectively that we observed. Both occurred with similar frequency. *G. geosporum*, which is not sporocarpic (Walker 1982), has

the lowest mean abundance and smallest abundance range.

One or more *Glomus* species occurred in 42 samples. Almost half of these samples (45.2%) had a total of >1000 spores/0.1 g feces (Fig. 2B). The median number was 712 *Glomus* spores/0.1 g feces. We estimated that one sample contained as many as 3.72×10^4 *Glomus* species A chlamydo spores/0.1 g feces. In another sample that contained 1.74×10^4 *G. macrocarpum* spores/0.1 g feces, these large spores comprised 5.4% of fecal dry mass, and, together with the *S. coremioides* sporocarps in the sample, constituted 7.3% of fecal mass.

Based upon monthly average abundances of sporocarps and spores in feces, we estimate that on average *Proechimys* defecate 79.1 *S. coremioides* sporocarps·g⁻¹ feces·d⁻¹ and 1.80×10^4 *Glomus* spores·g⁻¹ feces·d⁻¹. *Oryzomys* pass 88.3 *S. coremioides* sporocarps and 2.92×10^4 *Glomus* spores·g⁻¹ feces·d⁻¹. At 1.345 g dried feces·d⁻¹·100 g⁻¹ body mass of *Proechimys* (L. H. Emmons, unpublished data), and assum-

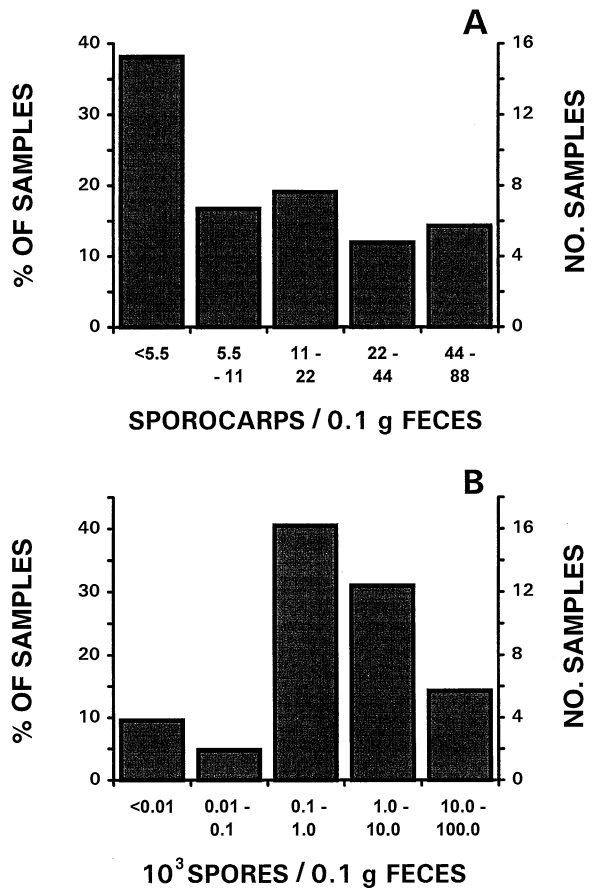


FIG. 2. Abundance of (A) *Sclerocystis coremioides* Berk. & Broome sporocarps not including loose spores (total sporocarps per 0.1 g air-dry feces) in 42 fecal samples that contained this fungus, and (B) four *Glomus* species (total spores per 0.1 g air-dry feces $\times 1000$) in 42 samples that contained this genus.

TABLE 1. Occurrence of *Glomus* species in 87 fecal samples from Peruvian Amazonian rodents of the genera *Proechimys* and *Oryzomys*.

	Species A	<i>G. macrocarpum</i>	<i>G. geosporum</i>	<i>G. microcarpum</i>
Spore diameter (μm)*	44.6	80.9	158.1	35.2
Frequency (no. of samples) [%]	27 [31.0]	22 [25.3]	11 [12.6]	10 [11.5]
Mean abundance (no. of spores)†	3920	1467	7	9405
Abundance range (no. of spores)	9–37 188	1–17 357	1–35	328–30 913

* Mean of length and width of at least 50 spores from our samples.

† In samples that contained spores; per 0.1 g air-dry mass of feces.

ing the same ratio for *Oryzomys*, at average densities (2.3 *Proechimys* and 1.8 *Oryzomys*/ha; Janson and Emmons 1990) and body masses at Cocha Cashu we calculate that the two rodent genera together defecate $10.04 \text{ g}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$. Extrapolating from this estimate, totals of glomaceous fungi passed in feces of the two rodent genera are 2.96×10^5 *S. coremioides* sporocarps and 7.30×10^7 *Glomus* spores $\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$.

Differences among rodent taxa

Proechimys samples contained a significantly greater frequency of *S. coremioides* (62.5%) and *Glomus* (60.0%) than did *Oryzomys* samples (36.2 and 38.3%, respectively) ($n = 87$, *S. coremioides* $G = 6.066$, $P = 0.014$; *Glomus* $G = 4.106$, $P = 0.043$). Among the four *Glomus* species that we found in feces, *G. macrocarpum* was found in a significantly greater proportion of fecal samples from *Proechimys* (37.5%) than *Oryzomys* (14.9%) ($n = 87$, $G = 5.906$, $P = 0.015$). Presence of *S. coremioides* or *Glomus* is not associated with rodent species, however, either within *Proechimys* (three species), or within *Oryzomys* (two species, excluding the single sample from *O. macconnelli*) (*Proechimys*: $n = 40$, *S. coremioides* $G = 0.362$, $P = 0.835$; *Glomus* $G = 1.073$, $P = 0.585$; *Oryzomys*: $n = 46$, *S. coremioides* two-tailed Fisher exact test $P = 0.655$; *Glomus* two-tailed Fisher exact test $P = 0.174$). Neither *S. coremioides* nor *Glomus* spp. presence is significantly associated with sex for all rodent species combined ($n = 75$, *S. coremioides* $G = 0.001$, $P = 0.980$; *Glomus* $G = 0.110$, $P = 0.740$). The distributions of number of fungus species per sample are significantly different between the two rodent genera (Fig. 1, Kolmogorov-Smirnov test, *Proechimys*, $n = 40$, *Oryzomys*, $n = 47$, maximum difference = 0.322, two-sided $P = 0.02$).

Seasonal patterns

Monthly occurrence of spores in *Proechimys* and *Oryzomys* feces are similar for *S. coremioides* (Fig. 3B and C) and all *Glomus* species combined (Fig. 3D and E). Occurrence of *S. coremioides* in *Proechimys* feces is significantly correlated with its occurrence in *Oryzomys* feces (Pearson $r = 0.632$, $n = 12$, $P = 0.028$). Although *Glomus* occurrence is not significantly correlated between the two rat genera (Pearson $r = 0.235$, $n = 12$, $P = 0.461$), similarity in months of low occurrence is apparent (Fig. 3D and E).

In both *Proechimys* and *Oryzomys*, *S. coremioides* occurrence is more frequent from January through July than from August through December, while *Glomus* occurrence is greater from April through September than from October through March (Fig. 3). Presence of *S. coremioides* and *Glomus* is significantly associated with months of peak abundance for each genus, respectively, when months are divided into two groups as described above ($n = 88$, January–July vs. August–December, *S. coremioides* $G = 37.707$, $P < 0.001$; $n = 88$, April–September vs. October–March, *Glomus* $G = 27.537$, $P < 0.001$). Neither genus of fungus is significantly associated with the months of peak abundance for the other ($n = 88$, January–July vs. August–December, *Glomus* $G = 3.471$, $P = 0.062$; $n = 88$, April–September vs. October–March, *S. coremioides* $G = 0.166$, $P = 0.683$).

Sclerocystis coremioides and *Glomus* occurrence are not correlated. Neither is significantly correlated with rainfall, fruit-fall, or seed production. Presence of *Glomus* spores in feces is significantly positively associated with the dry season (May–October during our study) ($n = 88$, $G = 10.974$, $P = 0.001$), but presence of *S. coremioides* is not ($n = 88$, $G = 3.572$, $P = 0.059$).

DISCUSSION

Our data suggest that rodents are important dispersers of mycorrhizal fungus spores in the Peruvian lowland wet forest that we studied. We estimate that 2.96×10^5 disaggregated *S. coremioides* sporocarps and 7.30×10^7 *Glomus* spores are passed annually per hectare in rodent feces at Cocha Cashu. All of the glomaceous species that we found in rodent feces, except for the new *Glomus* species, are known to form vesicular–arbuscular mycorrhizae.

This phenomenon is probably general, at least in the Neotropics. D. P. Janos (*personal observation*) has observed glomalean fungus spores in digestive tracts and feces of rodents from Costa Rica, Panama, and the Galapagos Islands. Spores are likely to be viable after passage through rodent digestive tracts (e.g., Trappe and Maser 1976, Warner et al. 1987).

Although Dowding (1959) proposed that rodents inadvertently ingest spores by eating insects that have consumed spores (e.g., Rabatin and Stinner 1991), evidence suggests that rodents deliberately consume

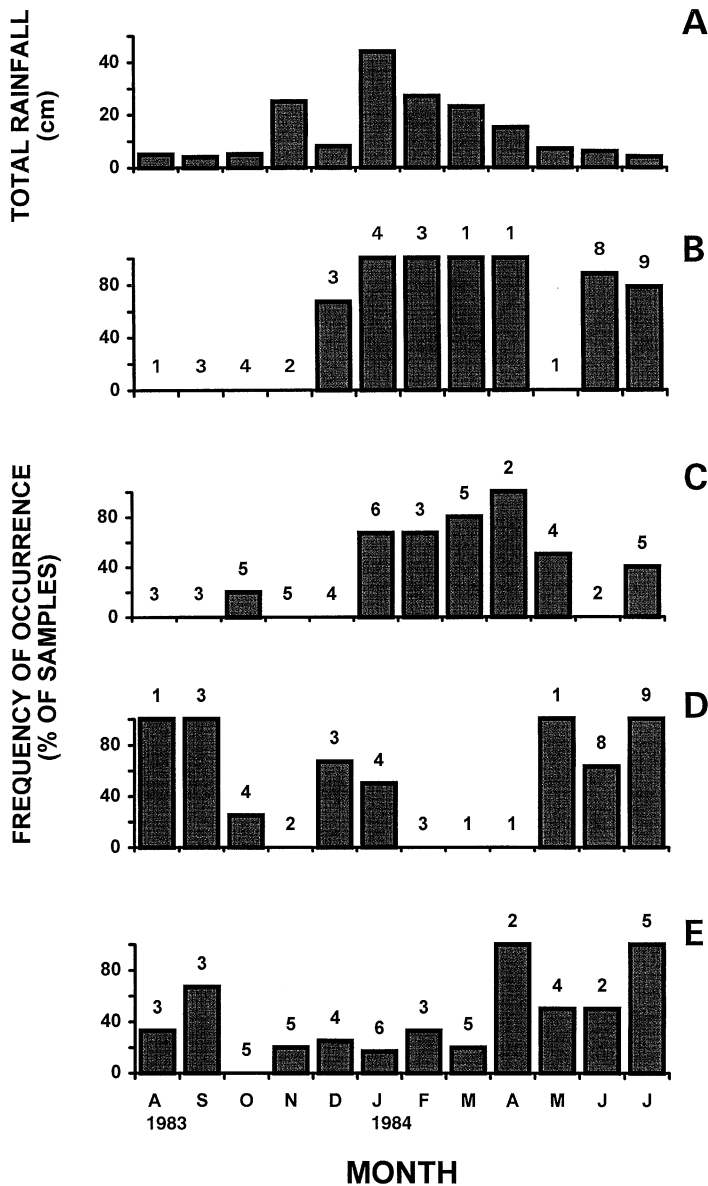


FIG. 3. (A) Total monthly precipitation (1 yr, August 1983 through July 1984; L. H. Emmons, unpublished data) at Cocha Cashu field station, Manu National Park, Madre de Dios Department, Peru, and monthly frequency of occurrence (percent of samples) of (B) *Sclerocystis coremioides* Berk. & Broome in feces of *Proechimys* spp., (C) *Sclerocystis coremioides* Berk. & Broome in feces of *Oryzomys* spp., (D) four *Glomus* species in feces of *Proechimys* spp., and (E) four *Glomus* species in feces of *Oryzomys* spp. collected at Cocha Cashu during the period for which precipitation is illustrated. Number of samples is shown above each bar.

glomalean fungus sporocarps. VAM fungi may facilitate and promote rodent mycophagy by forming sporocarps and sporocarp aggregations at the soil surface, by emitting attractive odors from sporocarps, and by providing a nutritional reward (see Gerdemann and Trappe 1974). Among 82 described species of *Glomus* and *Sclerocystis*, $\approx 46\%$ are known to form sporocarps (Almeida and Schenck 1990, Schenck and Pérez 1990). All glomalean fungi found by Maser et al. (1978) in the digestive tracts of >400 small mammals were sporocarpic species. Similarly, Gerdemann and Trappe (1974) noted that all the glomalean fungi found in the stomachs of three species of Pacific Northwest rodents were sporocarpic. These authors argued that glomalean fungus mycelium including sporocarp peridia is digested but spores pass unharmed through rodent guts.

Among the fungus species that we encountered in fecal samples, *G. macrocarpum* and *G. microcarpum* form sporocarps (Berch and Fortin 1983, 1984). We occasionally found clusters of spores of *Glomus* species A. This observation, together with abundant spores in feces, suggests that *Glomus* species A also is sporocarpic. Although *Sclerocystis coremioides* sporocarps are probably too small for a rodent to easily manipulate, they often occur in dense aggregations that can be a centimetre across and are sometimes covered by an encompassing hyphal peridium (Gerdemann and Trappe 1974, Almeida and Schenck 1990). In contrast, the two fungus species that we found least abundant in feces, *G. geosporum* and an *Entrophospora*, are not likely sporocarpic (see Walker 1982, Schenck and Pérez 1990). These might be ingested if mycorrhizal ad-

ventitious roots are gnawed by *Proechimys* nesting under tangled masses of vines (see Emmons 1982), or with insects. Although ingestion of *G. geosporum* and *Entrophospora* sp. may be inadvertent, we believe that rodents deliberately consume sporocarps of other Glomineae.

Seasonal patterns

We believe that sporulation of glomalean fungi may be seasonal at Cocha Cashu. Although seasonal absence of the fungi in feces could result from rodent diet shift to other, preferred foods, two aspects of our study suggest that rodents consume *Sclerocystis* and *Glomus* when sporocarps are present in the habitat. First, general agreement exists between *Proechimys* and *Oryzomys* (Fig. 3), even though the broad peaks of occurrence of *Sclerocystis* and *Glomus* in feces are not congruent. A diet shift between the two fungus genera might produce this pattern only if *Glomus* were preferred to *Sclerocystis* in August and September, but *Sclerocystis* were preferred to *Glomus* in January through March. Moreover, such a shift in preference would have to occur simultaneously for both rodent genera.

Second, consumption of glomalean sporocarps is not related to availability of other foods or rodent reproductive status. A relationship might be expected if rodents shift their diets because of a decrease in an alternative food resource such as fruits, or because of increased energy needs during pregnancy and lactation. However, such a relationship is not apparent at the study site. For example, fruit pulp and seed production is generally high from December through February at Cocha Cashu (Janson and Emmons 1990) when *S. coremioides* sporocarps are consumed frequently. Although *Glomus* is frequently consumed during months of generally low fruit and seed production, neither *Sclerocystis* nor *Glomus* occurrence in feces is significantly correlated with fruit fall or monthly midpoint seed production. *Proechimys* breed during months of both frequent and infrequent *S. coremioides* ingestion (L. H. Emmons, unpublished data), although minimum breeding of *Oryzomys* during September through November (L. H. Emmons, unpublished data) does correspond with infrequent sporocarp consumption. Fungus consumption is not significantly associated with sex, however, for all rodent species combined.

In our study, the occurrence of *Glomus* spores in feces is significantly associated with the dry season (Fig. 3). Louis and Lim (1987) found apparently cyclic annual variation in spore density in soil of a tropical forest in Singapore, but asserted that their results could not be explained by a simple direct correlation with season. We did not find a statistical relationship between the occurrence of *S. coremioides* in feces and either monthly rainfall or season.

Biological significance

In phosphorus-poor lowland wet tropical forest soils, a majority of tree species probably require VAM for successful seedling establishment (Janos 1980a, 1987). In intact rain forest, seedlings likely obtain VAM primarily through fungus spread from root to root (Alexander et al. 1992), although such spread is sometimes limited (Janos 1992). A single host individual may associate with many glomalean fungus species, even with several simultaneously (see Allen 1991). Spores of VAM fungi most likely are important for fungus persistence when roots and hyphae die, and for relatively long-distance dispersal. Spore dispersal by rodents is likely to influence the dispersion and abundance of spore inocula, and may affect the likelihood of VAM formation and seedling establishment.

Spore dispersion in consequence of rodent dispersal depends upon habitat use by rodent taxa, defecation pattern, and diversity and abundance of viable spores in feces. *Proechimys* ingest glomalean fungi more often than do *Oryzomys*, but both genera pass similar numbers of sporocarps and spores per unit mass of feces, perhaps because when clusters of *S. coremioides* sporocarps or individual *Glomus* sporocarps are encountered they are eaten in entirety. Because *Proechimys* are larger and occur in higher density than *Oryzomys* (Emmons 1982), however, *Proechimys* pass more spores per unit area than do *Oryzomys*. With typically small home ranges of 0.5 ha or less (Emmons 1982, Guillotin 1982), *Proechimys* are most likely to concentrate and redistribute glomalean spores, especially in the treefall gaps which they favor as den sites (Emmons 1982). *Proechimys* do not occur in treeless areas such as pastures, and their absence may limit dispersal of spore inocula to such sites, which can lack mycorrhizal inocula when overgrazed (Janos 1980b, 1992). *Oryzomys* similarly prefer areas of dense undergrowth, but may climb to heights of 1–2 m to rest on a branch. *Oryzomys* thereby might provide inoculum for low epiphytes (see Janos 1993). Defecation around nests, or use of latrines (Maser et al. 1978) would especially concentrate spores.

Our data document the role of rodents as spore dispersers in a lowland wet tropical forest. If the presence of spores in feces reflects the occurrence of sporocarps in the habitat, as we have argued, then *S. coremioides* and *Glomus* species sporulate seasonally with broad but disjunct peaks. Although the relative importance of spores vs. other types of mycorrhizal fungus inocula is poorly known, in tropical forests there is great importance of mycorrhizal mutualism among plants, fungi, and apparently, rodents.

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