TOWSON UNIVERSITY
COLLEGE OF GRADUATE STUDIES AND RESEARCH

AN EXPERIMENTAL TEST OF SMALL MAMMAL DISPERSAL OF ARBUSCULAR MYCORRHIZAL FUNGI SPORES

by

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A thesis

presented to the faculty of

Towson University

in partial fulfillment

of the requirements for the degree

Master of Science

Department of Biological Sciences

Towson University

May 2013

TOWSON UNIVERSITY
COLLEGE OF GRADUATE STUDIES AND RESEARCH

THESIS APPROVAL PAGE

This is to certify that the thesis prepared by John G. Zaharick Jr. entitled: An experimental test of small mammal dispersal of arbuscular mycorrhizal fungi spores, has been approved by her committee as satisfactory completion of the requirement for the degree of Master of Science.

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ACKNOWLEDGMENTS

I thank my major advisor Dr. Harald Beck for guiding me through my research, helping me attain funding, and bringing me into the scientific community. I am grateful to the members of my committee, Drs. Vanessa Beauchamp and Joel Snodgrass, for their intellectual contributions and support in experimental design and providing resources.

Thanks to Caitlin Graff for field training, advice, and assistance, Al Henneman for allowing me to conduct research on his property, and Dr. Don Forester for assistance in working at the Towson University Field Station. Thanks to field assistants Anthony Cannavino, Dawn Engel, Kristen Gazzara, Rachel Hebert, Mickey Kopansky, Bethany Link, April Marcangeli, Kerry Michael, Lacie Motier, Jennie Peterson, Andrew Simon, Ben Summers, and Nicolette Wentz

This project was funded by Sigma Xi Grants-in-Aid of Research, the Towson University Graduate Student Association, and the Towson University Faculty Development and Research Committee.

ABSTRACT

An Experimental Test of Small Mammal Dispersal of Arbuscular Mycorrhizal Fungi Spores

John G. Zaharick Jr.

Arbuscular mycorrhizal fungi (AMF) affect the structure of plant communities by influencing plant survivorship, growth, and diversity. Many AMF species produce spores below ground that have no obvious means of dispersal. Small mammals feed on AMF spores and those spores can still inoculate plants after passing through digestive systems. For this reason, small mammals are hypothesized to disperse AMF spores; however, few data exist to support this idea. I tested the ability of small mammals to disperse AMF spores by examining their impact on mycorrhizal inoculum potential in a northeast mesophytic forest. A field survey determined that small mammals sporadically consumed AMF spores. In a field experiment, more plots that were accessible to small mammals contained AMF than control plots, which excluded small mammals. This study provides experimental evidence that small mammals disperse AMF spores in a patchy manner, and wind dispersal also plays a role in AMF dispersal.

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Introduction

Mycorrhizal symbiosis influences numerous aspects of plant, soil microbe, and soil invertebrate communities. In addition to providing nutrients, minerals, and water to plant hosts in exchange for carbon compounds (Leake et al. 2004, Webster and Weber 2007), mycorrhizal fungi enhance plant productivity and resistance to pathogens (Song et al. 2010, Webster and Weber 2007). Mycorrhizal fungi are known to connect the root systems of plants, facilitating chemical signaling and allowing the transfer of nutrients, hormones, and warnings of predation and disease between individual plants (Song et al. 2010, Whittingham and Read 1982). Plant community diversity can either increase or decrease with the introduction of mycorrhizal fungi (Hartnett and Wilson 1999, Leake et al. 2004), and the fungi enhance allelopathy (Barto et al. 2012). Some endangered plants require certain mycorrhizal fungi species for survival (Bothe et al. 2010, Fuchs and Haselwandter 2004), and mycorrhizal fungi influence the ability of non-native plants to invade communities (Allen et al. 1989, Allen and Allen 1990).

Below ground, higher nutrient concentrations, microbial biomass, and numbers of microarthropods, nematodes, and protozoans are found in soil containing mycorrhizal fungi when compared to soils without them (Cromack et al. 1988, Entry et al. 1992). Soil stability is enhanced by both extraradical hyphae and the fungal protein glomalin, which causes aggregation of soil particles (Bedini et al. 2009, Coleman et al. 2004). Mycorrhizae may also act as a carbon sink. For example, plants respond to elevated atmospheric CO_2 levels by increasing photosynthesis, and greater production of carbohydrates occurs in mycorrhizal plants than non-mycorrhizal plants (Rillig and Allen 1999). Plants send the majority of carbon compounds below ground, as seen in northern

boreal forests where 50–70% of stored carbon was found in roots and mycorrhizal fungi as opposed to leaf litter (Clemmensen et al. 2013).

These influences on communities depend on the distribution of mycorrhizal fungi species in ecosystems. Mycorrhizal fungi in general may be present throughout the soil, but particular species are not (Davison et al. 2012, Lovelock and Miller 2002). Ecotmycorrhizal fungi (ECM) are primarily associated with trees while the more common arbuscular mycorrhizal fungi (AMF) are primarily associated with herbaceous vegetation (Wang and Qiu 2006). Mycorrhizal fungi species occur in isolated patches around host plants (Peay et al. 2011), and spatial heterogeneity of AMF species has been shown to influence plant community composition (Davison et al. 2012, Read 1998). Therefore, the ability of mycorrhizal fungi to disperse may govern their distribution and ultimately, the distribution of plants.

Mycorrhizal fungi spores are dispersed by wind, water, and animals (Frank et al. 2006, Harinikumar and Bagyaraj 1994, Harner et al. 2009). While mushrooms and puffballs can directly release spores into the air, hypogeous (below ground) fungi have no obvious means of dispersing spores (Johnson 1996). However, mycophagist small mammals consume hypogeous spores of both AMF and ECM (Mangan and Adler 2000, Vernes and Dunn 2009), and spores remain viable and can inoculate plants after passing through digestive systems (Colgan and Claridge 2002, Johnson 1996, Reddell et al. 1997, Trappe and Maser 1976). For this reason, small mammals have been considered important for dispersing mycorrhizal fungi spores (Cázares and Trappe 1994, Frank et al. 2006, Vernes and Dunn 2009).

Only a few experimental field studies have investigated the influence of small mammals on mycorrhizal fungi dispersal. For example, following the 1980 volcanic eruption of Mt. St. Helens (Washington, USA), the surrounding forest was covered by sterile ash and rock. Aerial spore traps only collected AMF spores when they were within a few meters of *Thomomys talpoides* Richardson (Pocket Gopher) mounds (Allen 1987). When Pocket Gophers were placed in enclosures, plants within the fencing became inoculated with AMF whereas plants immediately outside the enclosures remained AMF free (Allen and MacMahon 1988). In contrast, mammals played a minimal role in dispersal compared to that of wind in an open shrub-steppe community (Warner et al. 1987).

Animal effects on AMF communities were found in an Australian rainforest where small mammal exclosures had lower mycorrhizal inoculum potential, spore abundance, and spore species richness after a 3-year period than accessible controls (Gehring et al. 2002). It was not clear though whether small mammals were directly dispersing spores or indirectly increasing mycorrhizal levels by killing seedlings and severing roots, as dead roots may act as a greater source of inocula than living roots (Gehring et al. 2002).

Because of the inconclusive nature of the previous studies, further research is necessary to verify whether mycorrhizal fungi spores are dispersed by small mammals. If small mammals are the primary vector of mycorrhizal fungi dispersal, then they may play a critical ecological role in the distribution, fitness, and species richness of mycorrhizal plants (Gehring et al. 2002, Leake et al. 2004), levels of soil nutrients, and abundance of soil fauna (Coleman et al. 2004). Small mammals may also be necessary for dispersing

mycorrhizal fungi spores to areas where mycorrhizal activity has been reduced after disturbance, such as by wind throws, landslides, fires, floods, herbivore browsing, or human activities (Boerner et al. 1996, Bressette et al. 2012, Fisher and Fulé 2004, Perry et al. 1987, Wearn and Gange 2007).

In this study, I trapped small mammals in a northeast mesophytic forest over 2 years and examined fecal and fur samples for AMF spores to test both endo- and epizoochory as mechanisms of spore dispersal. In addition, I conducted a field experiment to test the ability of small mammals to disperse AMF spores. I placed trays of sterile soil in forest plots that were accessible to small mammals and either baited or non-baited from May to September 2012. These plots were compared with control plots that excluded small mammals via an aluminum flashing wall and window screen. I hypothesized that soil in accessible plots would have a higher mycorrhizal inoculum potential after 5 months compared to exclosure plots.

Materials and Methods

Study Area

The study site is located at the Towson University Field Station in Monkton, Maryland (39°35'57"N, 76°38'13"W), which comprises 92 ha of closed canopy mesophytic forest. To the northwest and southeast the field station connects to a riparian forest that forms the 7,200 ha Gunpowder Falls State Park (Fig. 1). As part of a continuous forest instead of an isolated patch within a matrix of agrarian and developed land, the TU Field Station is open to the dispersal of organisms from the surrounding state park. Therefore, the field station is ideal for experimental ecological research.

Small Mammal Trapping

To assess what small mammal species were present at the TU Field Station, and to assess their ability to disperse AMF spores via endo- or epizoochory, I conducted small mammal trapping in April, June, August, and October of 2011 and 2012. Three trapping grids were established along a southwest-northeast transect in the central portion of the TU Field Station. Camp Puh'Tok, a children's camp, borders the western edge of the field station and grids were situated to avoid human activity. Grids were approximately 150 m apart (Fig. 2). Each grid consisted of 100 Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, FL) in a 10 x 10 arrangement with 10 m between traps. Grids contained 50 large traps (8.9 x 7.6 x 22.9 cm) and 50 small traps (5.1 x 6.3 x 16.5 cm) placed in an alternating pattern. Bait used in traps contained equal parts peanut butter, paraffin wax, rolled oats, and raisins (Calhoun 1959). Polyester stuffing was added to traps in April and October to serve as nesting material when nighttime temperatures fell close to freezing.

In 2011, I surveyed all 3 grids in a sampling month. Traps were placed in a single grid at a time and checked for 4 consecutive days beginning at sunrise. I re-baited and reset traps as needed. I then moved traps to the next grid along the transect. The order in which grids were surveyed was shifted each month to avoid sampling bias. During the 2012 trapping season, I surveyed only 1 grid per sampling month to verify the findings in 2011.

I identified captured animals to genus or species. I assessed sex and reproductive condition, recording in males testes ascended or scrotal and in females vagina open or closed, nipples large or small, and pubic symphysis open or closed. I measured mass with 100 g and 500 g spring scales (Pesola Ag, Baar, Switzerland) and attached a uniquely numbered 1005-1 monel ear tag (National Band and Tag Company, Newport, KY) to each animal before release. I recorded the trap location of all captures and the ear tag number of previously marked individuals. The protocol for handling mammals followed the guidelines for using mammals in research (Sikes et al. 2011).

I collected fecal samples from animals while they defecated during handling. Fecal pellets were stored in either a glass vial or plastic microcentrifuge tube and transported to the TU laboratory where they were refrigerated at 4ºC. I did not collect fecal samples from traps because traps were potentially exposed to multiple individuals. I collected 1 fecal sample per individual once per month.

Depending on size, 2 to 3 fecal pellets were ground and stirred in a glass vial containing 75% ethanol. I filtered the resulting mixture twice using 250 µm and 45 µm U.S.A. standard test sieves (Newark Wire Cloth Company, Clifton, NJ). Material from the 45 µm sieve was rinsed into a Petri dish and examined at 20x magnification using a

dissecting microscope (Mel Sobel Microscopes Ltd., Hicksville, NY). I transferred spores found in the dish via pipette to a microscope slide containing a drop of Melzer's reagent for preservation and identification (Maser et al. 1978).

To investigate the possibility of epizoochory, I collected fur samples using a piece of transparent adhesive tape placed against each animal, covering the ventral and dorsal surfaces. Tape samples were then affixed to a microscope slide in the field and examined at 100x magnification with a compound light microscope (Zeiss, Oberkochen, Germany) in the lab for the presence of AMF spores.

Aerial Spore Sampling

To determine the abundance and seasonal variation of AMF spores dispersed by wind, I placed 8 Petri dishes (15 x 1.5 cm) containing adhesive paper in each trapping grid in April, June, August, September, and October 2011. I divided each grid into 4 segments and randomly placed 2 dishes within each segment at locations flagged for Sherman traps for a 48-hour period (Allen 1987). Dishes were laid flat on the forest floor. After exposing Petri dishes to the air at the field station, I examined them at 20x magnification and transferred AMF spores to microscope slides containing Melzer's reagent for preservation and identification.

Experimental Procedure

I quantified mycorrhizal inoculum potential in soil exposed to small mammals at the TU Field Station. Data from the 2011 field survey indicated that AMF spores occurred in small mammal feces during June and August, but not in April or October. Therefore, the experiment was carried out from May through September 2012.

I established 10 plots at the field station (Fig. 2). I placed 10 parallel lines over a map of the field station, with approximately 50 m between lines. One plot was placed on each line, randomly along the length. Straight-line distance between plots was at least 90 m to reduce the likelihood of the same small mammal visiting multiple plots. Trapping data indicated that the primary member of the small mammal community was *Peromyscus* spp., which have home ranges of on average 590 m^2 (Wolff 1985), and *Peromyscus leucopus* in Maryland are known to travel 30 to 84 m away from their burrows while foraging (King 1968).

Each plot contained 3 subplots 1 x 1 m in size with 10 m between subplots (Fig. 3). Two experimental subplots were accessible to small mammals and 1 control subplot excluded them. To encourage small mammal activity, 1 open subplot contained bait of the same mixture used in trapping, while the other open subplot was not baited. I placed bait in subplots once per week from May to the end of September 2012.

Small mammal exclosures consisted of aluminum flashing approximately 60 cm above and 10 cm below ground to prevent mammals from entering beneath the flashing. Two pieces of rebar in each corner of the subplot supported the flashing, with one inside the structure and one outside, tied together with wire. Window screen, held by staples, covered the tops of exclosures and prevented mammals from entering.

Each subplot contained a single plastic tray (56 x 28 x 5.5 cm) filled with soil sterilized in the TU greenhouse in an electric soil sterilizer (Pro Grow Supply Corporation, Butler, PA) by heating it to 82°C for 2 hours (Kawamoto and Habte 2011). Plastic trays were placed in shallow depressions to be level with the ground.

All sites occurred on uneven surfaces, and AMF spores present in the soil could be dispersed by rainwater flowing across the forest floor. Therefore, u-shaped plastic rain guards were placed 50 cm uphill of accessible subplots to redirect surface flows of rainwater away from subplots. Metal hexagonal fencing was placed over soil trays and held down with metal stakes to prevent large mammals from digging in subplots and displacing soil.

A 20 cm long, 10 cm diameter, longitudinally cut piece of green PVC pipe was placed in each subplot to serve as shelter for animals because small mammals typically avoid open spaces where they are vulnerable to predators (Catall et al. 2011, Perea et al. 2011). I autoclaved pipe sections at 121°C for 30 minutes to avoid contamination of the experimental soil.

To monitor aerial spore deposition near subplots and assess its contribution to inoculum potential, I placed 1 aerial spore trap within 1 m of each subplot for a 7-day period each month for the 5 months of the experiment. I checked exclosures once a week for damage and conducted repairs as needed.

To document whether small mammals actually interacted with soil trays, I deployed motion-activated cameras (Moultrie Game Spy digital trail camera model D-40) on baited subplots for a 1-week period each month from May to September 2012. Cameras were attached to wooden stakes or rebar with bungee cords at a height of approximately 45 cm. The cameras were set to take 3 photographs after each trigger event with a 5-minute delay between events. Two strips of duct tape were placed over camera flashes, creating an opening approximately 2 to 3 mm wide, to reduce glare in photographs.

I took a 1-L soil sample from the surface of each of the 30 subplots as this is where feces would be found. I collected soil during the first week of October 2012 and transferred it to the Towson University greenhouse. Soil was placed in bleach disinfected Deepots where *Sorghum bicolor drummondii* (Nees ex Steud.) de Wet and Harlan (Sudangrass) was grown as part of a bioassay to detect mycorrhizal inoculum potential. Inoculum potential is an effective measure of mycorrhizal fungi levels in soil (Anderson et al. 2010).

Thirty days after seed germination, I harvested plants, removed fine roots, and fixed them in 75% ethanol (Beauchamp et al. 2006; Fracchia et al. 2011). Roots were cleared in 5% KOH and stained in Trypan blue (Koske and Gemma 1989) and then placed on microscope slides containing polyvinyl alcohol lactoglycerol mounting medium (INVAM 2013). I measured root length colonization by mycorrhizal fungi using the grid line intersect method (Giovannetti and Mosse 1980).

Statistical Analysis

To generate small mammal population estimates at the TU Field Station, I used the Lincoln-Peterson index (Lancia et al. 1994), with Bailey's modification to correct for statistical bias caused by small sample size (Bernard and Hansen 1992), on the ratio of total captures to total recaptures every trapping month.

I used a null hypothesis statistical testing approach to examine differences between experimental treatments with significance set to $p < 0.05$. The low number of fungal infections detected limited my ability to use statistical models such as analysis of variance or a mixed effects linear model. However, any fungi that appeared in the sterilized soil were biologically significant because the organisms had to disperse into the

experimental trays. Therefore, instead of analyzing the number of root infections, I performed a Fisher's Exact test (Upton 1992) to examine presence/absence of fungi. The test was run in software program R (R Development Core Team 2009) with treatment type as the independent variable and presence of fungi as the dependent variable.

Results

Seven small mammal species were documented at the TU Field Station: *Peromyscus* spp. Gloger (Deer Mice), *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel), *Microtus pinetorum* LeConte (Woodland Vole), *Tamias striatus* Linneaus (Eastern Chipmunk), *Blarina brevicauda* Say (Short-Tailed Shrew), and *Glaucomys volans* Linnaeus (Southern Flying Squirrel) (Table 1). *Peromyscus maniculatus* Wagner (Deer Mouse) and *Peromyscus leucopus* Rafinesque (White-Footed Mouse) could not be distinguished in the field. Therefore, I grouped them at the genus level.

Peromyscus spp. composed 86.8% of all captures. Population size at the TU Field Station within an 8100 m^2 trapping grid ranged from 9–51 individuals with a mean of 30.5 individuals. In 2011, population size increased across all 3 trapping grids from June to October. In 2012, population size increased from April to August and then decreased into October (Table 2; Fig. 4).

All AMF spores were identified to the genus *Glomus* L.R. and C. Tulasne and further classified into 8 morphospecies based on color, spore size, and spore wall thickness. Two spores were too degraded to group as morphospecies. One morphospecies was only found in August and September and another morphospecies was only found in *M. pinetorum*. No other morphospecies grouped by date or small mammal species.

A total of 353 AMF spores were detected among 71 samples of small mammal feces in June and August 2011. Spore frequency varied, with 9 fecal samples containing a single spore and 2 samples containing over 100 spores. A total of 12 AMF spores were detected among 57 samples in 2012 in June and October. *Peromyscus* spp. and *M.*

pinetorum contained the majority of spores detected (Table 3). One *S. carolinensis* sample contained 1 spore in June 2011.

Adhesive tape used to investigate epizoochory picked up mammal fur and ectoparasites, but out of 223 samples only a single AMF spore was detected on a *Peromyscus* sp. in June 2012.

The 120 aerial spore traps placed in grids in 2011 collected a total of 4 spores, in April and September. The 150 aerial traps placed near experimental subplots in 2012 collected 15 spores, 7 of which were in August (Table 4).

Rain filled aerial traps with water each month in 2012. Conducting aerial spore collection for 7 days in 2012 compared to 2 day intervals in 2011 increased odds of precipitation occurring while they were in the field. Water usually evaporated before the end of the 7-day exposure, but in August traps were left exposed for 2 weeks in an effort to let water evaporate. Traps could not be replaced because new Petri dishes would be rained on as well, and moving traps risked pouring contents out of the dish.

AMF spores dispersed via wind at a rate of 0.77 spores/m^2/day in 2011 and 0.74 spores/m^2/day in 2012. Other material found in aerial traps included pollen, fern spores, microinvertebrates, and two *Diadophis punctatus* Linneaus (Ringneck Snake).

At 4 of the subplots where wind dispersing spores were detected, AMF also appeared in the bioassay. Six plots where wind dispersed fungi were detected contained no AMF in the bioassay. In 7 subplots with AMF in the soil, no wind dispersing spores were detected (Table 5).

Camera traps aimed at baited subplots documented *Peromyscus* spp., *S. carolinensis*, and *Procyon lotor* Linnaeus (Raccoon) at all baited subplots. *Tamias*

striatus, *Didelphis virginiana* Kerr (Virginia Opossum), *Marmota monax* Linnaeus (Groundhog), and *Felis catus* Linnaeus (Feral Cat) also appeared at plots (Table 6).

Experimental subplots contained more AMF infections than controls (4 baited, 5 non-baited, 2 control). However, error bars for a plot of the means of percent root infection overlap (Fig. 5).

In 4 subplots, roots from the surrounding soil grew into soil trays from below though drainage slots. AMF was detected in 2 subplots in which foreign roots entered the sterilized soil. Unknown animals broke into 4 exclosures and disturbed the sterilized soil. One of those exclosures contained AMF and the other 3 did not.

All 20 open plots were pooled and compared to 10 closed plots in statistical analysis. Nine open plots contained AMF and 11 did not. Two closed plots contained AMF, while 8 did not. Applying Fisher's exact test, the proportion of open plots containing AMF was not significantly higher ($p = 0.25$) than the controls.

Discussion

Small mammals play key roles in ecosystems by serving as a food source for raptors, reptiles, and carnivorous mammals and as herbivores by preying upon and dispersing seeds (Kaminski et al. 2007). It is commonly accepted that they also disperse mycorrhizal fungi spores and are therefore critical in structuring plant communities and influencing successional processes (Cázares and Trappe 1994, Frank et al. 2006, Janos et al. 1995, Vernes and Dunn 2009). Although not statistically significant, my results suggest limited dispersal of AMF by small mammals in northeastern deciduous forests. Forty-five percent of accessible plots contained AMF versus 20% of exclosure plots. AMF spores were found in 3.6-16.7% of small mammals, twice in amounts of over 100 spores per sample.

Individuals of *Peromyscus* spp. and *M. pinetorum* that had 192 and 134 spores respectively in fecal samples show the ability of small mammals to disperse AMF spores in a more concentrated fashion than the wind, increasing the odds of viable spores being placed near plants (Maser et al. 1978). That concentrated mass also makes mammalian spore dispersal patchy, as opposed to a more even distribution in wind dispersal. This has the potential to affect plant succession by adding heterogeneity to the landscape. In an Estonian temperate forest, AMF richness and community composition varied spatially in plots 30 m away from each other, and the overlying plant community reflected this (Davison et al. 2012). Depending on what mycorrhizal species are dispersed into open habitat, succession could proceed toward persistence of AMF herbaceous vegetation or development of ECM forest (Schickmann et al. 2012).

Those large counts are exceptions in my data, however. Most fecal samples contained between one and 10 spores, and a low percentage of individuals were found to consume fungi. These findings fit a model in which small mammals are among many vectors of AMF, each dispersing a small amount of inocula, but in sum dispersing large amounts of fungal reproductive structures (Fig. 6). Collembola (springtails) disperse AMF hyphae fragments (Klironomos and Moutoglis 1999, Seres et al. 2007), Formicidae (ants) concentrate root fragments containing AMF in their nests (Friese and Allen 1993, Harinikumar and Bagyaraj 1994, McIlveen and Cole 1976), and in one study, Leporidae (rabbit) feces and whole individuals of Orthoptera (grasshoppers) inoculated plants with AMF (Ponder 1980). AMF spores have also been found in mud in nests of *Turdus migratorius* Linnaeus (American Robin), *Hirundo erythrogaster* Linnaeus (Barn Swallow), and Trypoxyloninae (mud dauber wasps) (McIlveen and Cole 1976).

Ectomycorrhizal spores remained viable after passing through *Harpaphe haydeniana* Wood (Yellow-spotted Millipede) and *Odocoileus hemionus* Rafinesque (Black-tailed Deer) (Ashkannejhad and Horton 2006, Lilleskov and Bruns 2005). Ectomycorrhizal spores were also found to have intact nuclei after passing through Oribatida (mites), Collembola, Diptera (fly larvae), Coleoptera (beetle larvae and adults), Chilopoda (centipedes), and *Taricha* sp. Gray (Pacific Newt), but viability was not tested (Lilleskov and Bruns 2005).

Johnson (1996) suggested spores could disperse by the wind after being exhumed by small mammals. Ants have also been cited in this capacity (Harinikumar and Bagyaraj 1994, McIlveen and Cole 1976). Wind has been found to disperse spores up to 2 km in open habitat (Allen et al. 1989, Warner et al. 1987). Spores and hyphae can also

be transported in flood deposits, dispersing potentially up to 100 km (Harner et al. 2009). Such dispersal would be restricted to riparian areas, however.

Small mammal dispersal of AMF spores occurs through endozoochory as opposed to epizoochory. One *Glomus* spp. spore was found among 223 fur samples. While epizoochory has been studied in invertebrates (Lilleskov and Bruns 2005), this was the first study to test epizoochory as a dispersal mechanism for AMF in small mammals.

I encountered *Peromyscus* spp. at every baited subplot in the field experiment. While wind dispersing spores may have inoculated some subplots, fungi did not appear in the experimental soil in six subplots where spores were detected in the air. A third potential source of AMF in the field experiment includes fungi present in plant roots that entered experimental trays. The top layer of soil was taken from every subplot, as that is where fecal matter was expected to be found. The influence of foreign roots growing from below may have been minimal as most of the soil they contacted was not collected.

While the data presented here suggest that small mammals dispersed AMF spores into sterile soil plots, the results are not conclusive due to the lack of control of other sources of AMF spores and the lack of statistical significance in the experiment. Future experiments that control for wind dispersal of spores and presence of plant roots could provide stronger evidence of small mammal dispersal of spores. In addition, the percentages of fungi that appeared in the bioassay were low, which hindered the ability to conduct statistical analysis. Sterile soil was exposed to field conditions for 5 months. A longer exposure time may increase the signal size of AMF. Ectomycorrhizal spores have been found to survive at least 6 years in soil in field conditions (Nguyen et al. 2012), suggesting sterile soil trays could accumulate vital spores in a multi-year experiment.

Direct comparisons between mammalian and wind dispersal rates could not be made because rate of defecation was not measured. Janos et al. (1995) determined that *Proechimys* spp. J.A. Allen (Spiny Rats) defecated 1.3 g dried feces/day/100 g body mass in a Peruvian Amazon rainforest. Defecation rates for *Peromyscus* spp. are unknown however. While *Proechimys* spp. and *Oryzomys* spp. Thomas (Rice Rats) were calculated to disperse 7.30×10^7 *Glomus* spores/ha/yr, Janos et al. (1995) found AMF in 69.3% of all fecal samples. I observed AMF in only 6.6% of fecal samples, implying a much lower rate of dispersal than what may occur in the Peruvian rainforest.

To compare dispersal rates indirectly, *Glomus* spp. spores precipitated from the air at a consistent rate both years: 0.77 spores/m^2/day in 2011 and 0.74 spores/m^2/day in 2012. In contrast, mycophagy varied between years. In 2011, 14.3% of *Peromyscus* spp. and *M. pinetorum* dispersed spores in June and 16.7% in August. The proportion of small mammals detected consuming fungi decreased in 2012 to 6.9% in June and 3.6% in October. If this change reflects a real difference in mycophagy between years as opposed to a decrease in detection ability, then the relative influence of wind on AMF spore dispersal increased during the field experiment. AMF spores separate from soil at wind speeds of 0.5 m/s (Tommerup 1982). Any spores that reach the surface will be moved abiotically. However, hypogeous fungi have no obvious means of dispersing spores. Lower mammalian foraging activity should also reduce the number of spores exposed to the wind. Since the rate of aerial spore dispersal did not decrease, alternative mechanisms may be bringing spores to the surface.

If small mammal foraging for fungi did not change between years, then I detected a lower number of individuals consuming AMF for several possible reasons.

Mycorrhizal fungi can compose as little as 1% of *Peromyscus* spp. and *Microtus* spp. diet by volume (Whitaker 1962). The concentration of spores in *P. maniculatus* feces peaks <12 h after animals consume fungi and reaches half concentration in another 12 h (Cork and Kenagy 1989b). If small mammals consumed fungi, but fecal samples were taken after spores had already passed through their digestive systems, mycophagy would not have been detected. All spore counts in this study represent minimum counts for what small mammals are able to disperse. I used fewer traps in 2012, resulting in fewer fecal samples, which reduced odds of detecting mycophagy. I was also unable to trap large numbers of individuals from species other than *Peromyscus* spp. *Microtus* spp. are known to consume AMF (Maser et al. 1978), but only 4 individuals were trapped in 2 years. *M. pinetorum* is a common small mammal in Maryland forests (Escalante et al. 2010, Smolen 1981). Pitfall traps may be a better method for sampling this species (Mengak and Guynn 1987, Wilson et al. 1996).

Among the four species found to consume AMF, *Peromyscus* spp. were the most common, accounting for 86.8% of all captures. This is not surprising as *P. maniculatus* is the most widespread rodent in North America (King 1968, Lehmkuhl et al. 2008, Linzey 2008) and *P. leucopus* is one of the most abundant species in eastern North American forests (King 1968, Lackey et al. 1985, Linzey et al. 2008). *Peromyscus* spp. are generalists, found across numerous habitats, including forests, prairies, swamps, deserts, and scrublands (Adler and Wilson 1987, Brannon 2005, Linzey 2008, Peavey et al. 1997, Schweiger et al. 2000, Wywialowski 1987). As such, they have been hypothesized to disperse mycorrhizal spores across habitat types (Frank et al. 2009, Jones and Lindquist 2012, Miller and Getz 1977, Sidlar 2012) while other mycophagist small

mammals, such as *Clethrionomys gapperi* Vigors (Red-Back Vole), are habitat specialists (Terwilliger and Pastor 1999). The widespread distribution of *Peromyscus* spp. across the continent and generalist lifestyle suggests an important role in influencing a wide diversity of plant communities via AMF.

Previous research has shown that small mammal feces can inoculate vascular plants with AMF in greenhouse conditions (Trappe and Maser 1976, Reddell et al. 1997) and small mammals are able to positively influence the AMF community in the field (Gehring et al. 2002). The data presented here show that sterile soil exposed to small mammals in a mesophytic forest habitat became inoculated with AMF spores, and those spores were capable of associating with herbaceous plants. Further research is required, however, to distinguish between the numerous potential vectors of AMF inocula.

TABLE 1.-Small mammals trapped at the Towson University Field Station from April to October 2011 and 2012.

	Peromyscus spp.	*Sciurus carolinensis*	*Microtus pinetorum*	*Tamias striatus*	*Blarina brevicauda*	*Glaucomys volans*
Number of individuals (male/female/unknown[a])	81/63	7/2/3	3/0/1	2/0/3	0/0/1	0/1
% of total captured	86.8	7.2	2.4	2.4	0.6	0.6
% recaptured	78.5	25.0	50.0	0.0	0.0	0.0

[a] Individuals that escaped during handling or that were difficult to identify were not sexed.

TABLE 2.-Lincoln-Peterson Index with Bailey's modification estimates of *Peromyscus* spp. population size.

	Grid A	Grid B	Grid C	Total
June 2011	29	29	9	67
August	25	51	-[a]	76
October	36	26	23	85
April 2012	-[b]	20	-[b]	20
June	-[b]	-[a]	-[b]	-
August	-[b]	45	-[b]	45
October	-[b]	43	-[b]	43

[a] A population estimate could not be made when the number of recaptures in a month was 0.
[b] Grids A and C were not trapped in 2012.

TABLE 3.-Occurrence of arbuscular mycorrhizal fungi spores in *Peromyscus* spp. and *Microtus pinetorum*

	Jun. 2011	Aug. 2011	Jun. 2012	Oct. 2012
No. of samples [% containing AMF]	35 [14.3%]	36 [16.7%]	29 [6.9%]	28 [3.6%]
Median abundance (no. of spores)	1	1	3	6
Abundance range (no. of spores)	1-134	1-192	3	6

TABLE 4.-Number of arbuscular mycorrhizal fungi spores detected in aerial spore traps per month.

Month	AMF spores
April 2011	2
June	0
August	0
September	2
October	0
May 2012	2
June	1
July	4
August	7
September	1

TABLE 5.- Number of arbuscular mycorrhizal fungi spores detected in aerial spore traps placed at experimental subplots in 2012 and AMF infections detected in bioassay per subplot. Subplots that had no aerial dispersing spores or soil fungi are not listed.

Subplot	No. aerial spores	Fungi in bioassay (%)
2C	1	0.00
3C	2	0.00
4B	0	0.41
4C	0	4.09
5C	1	0.00
6B	4	9.75
6C	1	0.31
7A	1	0.30
7B	2	0.00
7C	1	0.32
8B	1	0.00
8C	0	14.51
9A	0	0.96
9B	0	3.69
9C	0	0.29
10B	0	2.32
10C	1	0.00

TABLE 6.-Visits detected by trail camera per baited subplot per species from May to September 2012.

Plot	*Peromyscus* spp.	*Sciurus carolinensis*	*Tamias striatus*	*Procyon lotor*	*Didelphis virginiana*
1	25	5	-	1	1
2	41	38	-	2	1
3	16	42	-	1	-
4	1	1	-	1	-
5	16	36	-	3	-
6 [a]	24	2	-	7	2
7	32	6	5	4	4
8	33	1	1	2	3
9 [b]	22	3	-	5	7
10	11	3	1	3	-

[a] A Groundhog (*Marmota monax*) was documented in plot 6.
[b] A Feral Cat (*Felis catus*) was documented in plot 9.

Figure 1.-Location of the Towson University Field Station in Baltimore County, Maryland. The 92 ha field station is part of a continuous forest that forms the 7,200 ha Gunpowder Falls State Park.

Figure 2.-Map of the Towson University Field Station in Maryland. Grids A, B, and C were trapped in April, June, August, and October 2011. Only Grid B was trapped in 2012. Circles 1-10 are experimental plots.

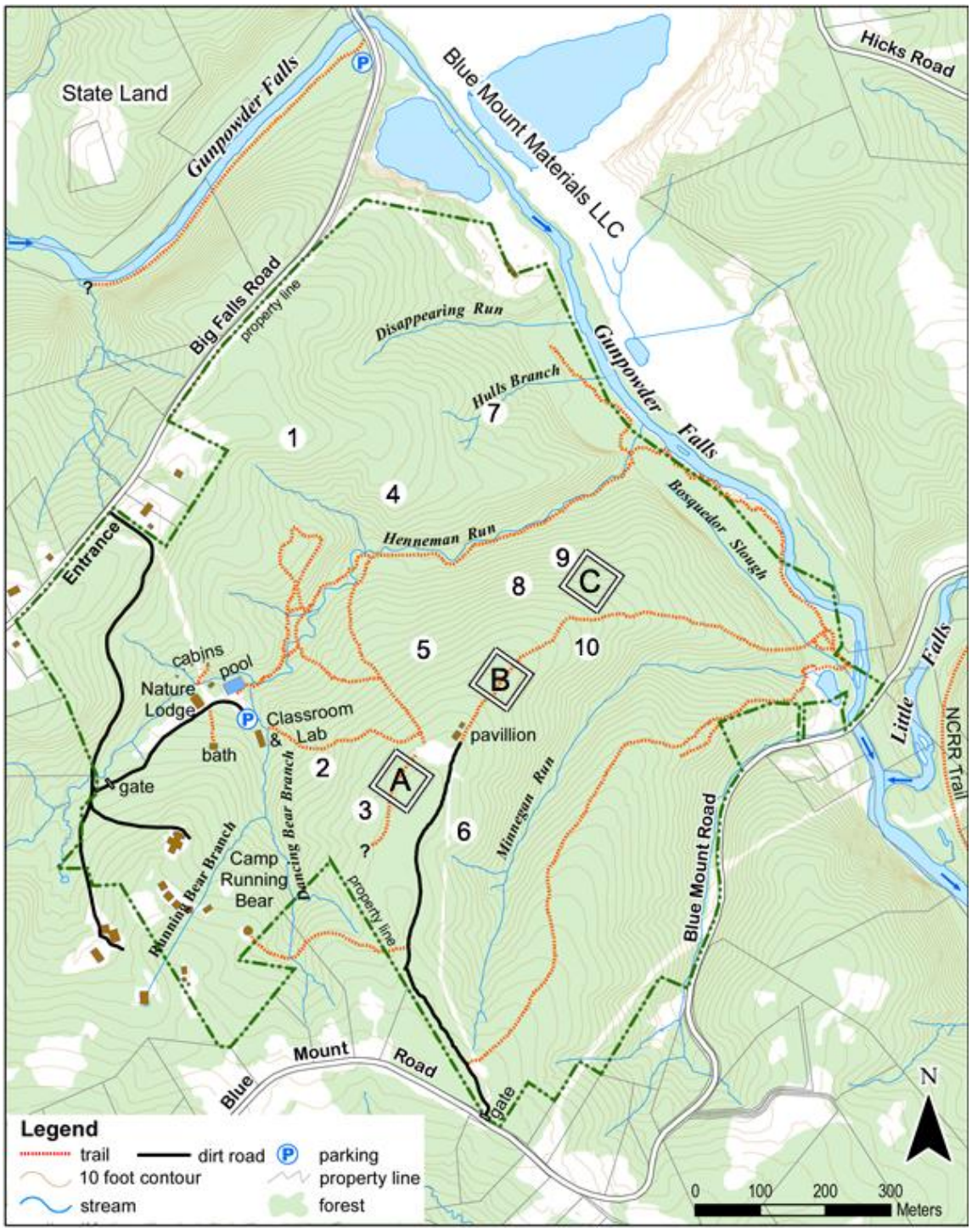


Figure 3.–Ten plots were established at the TU Field Station in Maryland. Two subplots were accessible (dashed lines) and one excluded (solid lines) small mammals with aluminum flashing and window screen. A u-shaped plastic rain guard was placed uphill of open subplots to divert rain runoff in which AMF spores may disperse. The order and alignment of subplots was randomly determined.

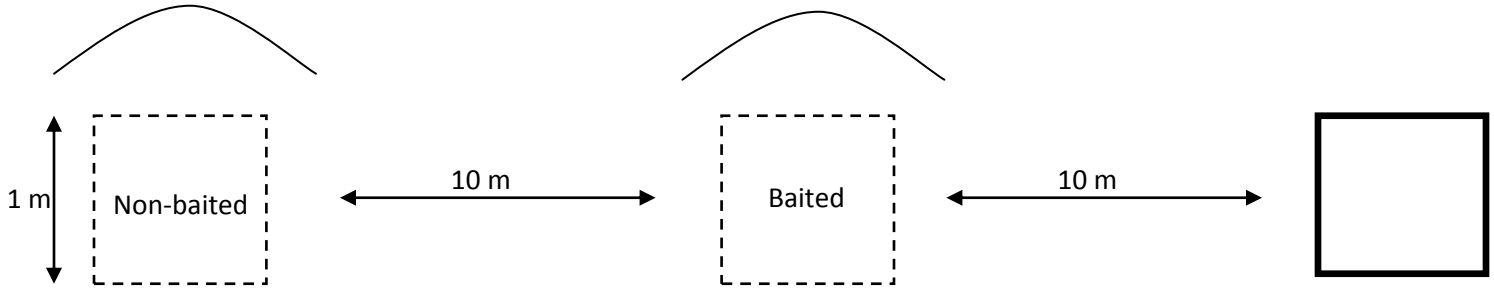


Figure 4.-Change in estimated population size of *Peromyscus* spp. from spring to autumn. Population estimates could not be made for April 2011 or June 2012 due to a lack of recaptures.

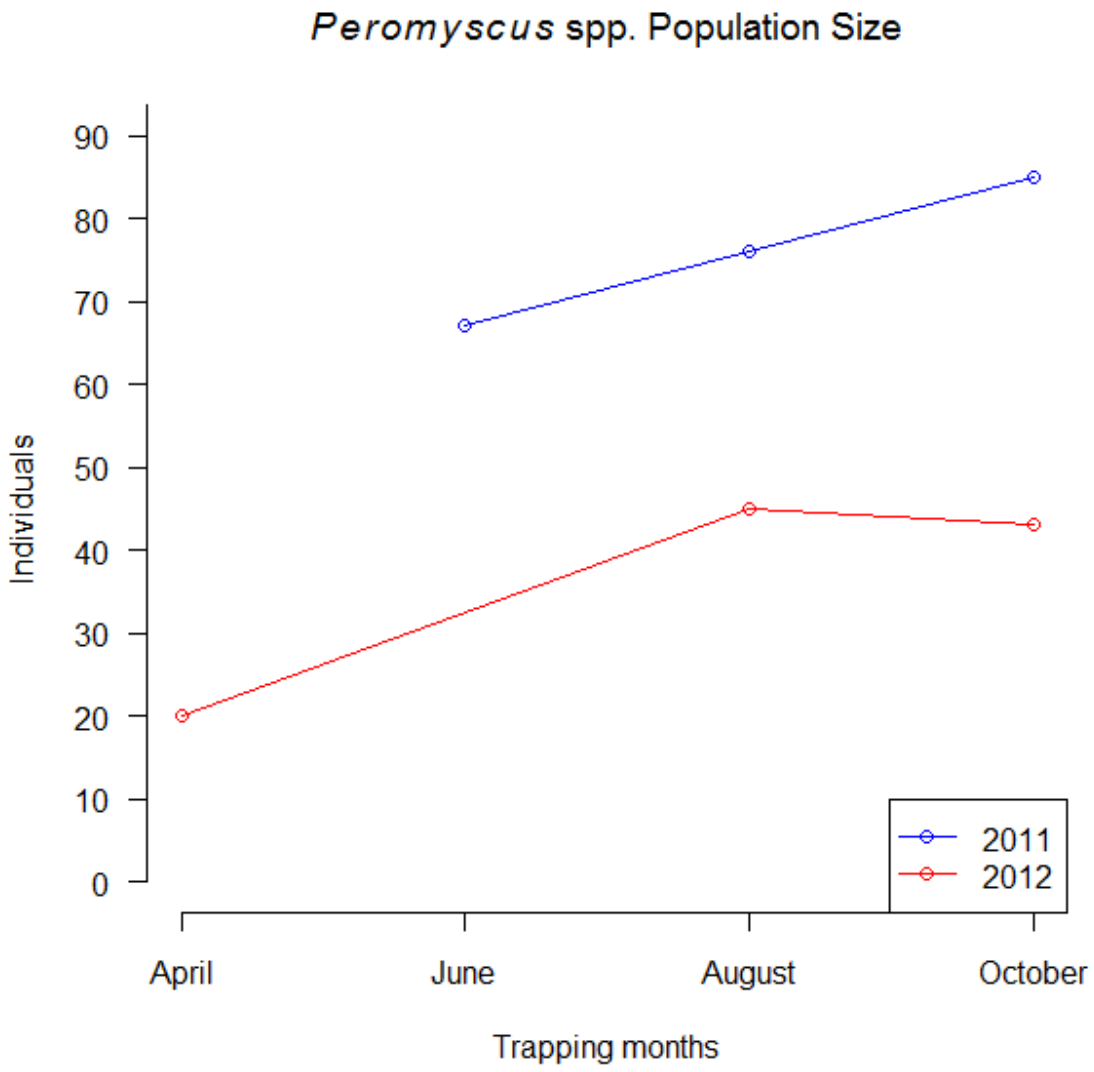


Figure 5.-Comparison of mean (±1 SE) percent root infection among treatment types.

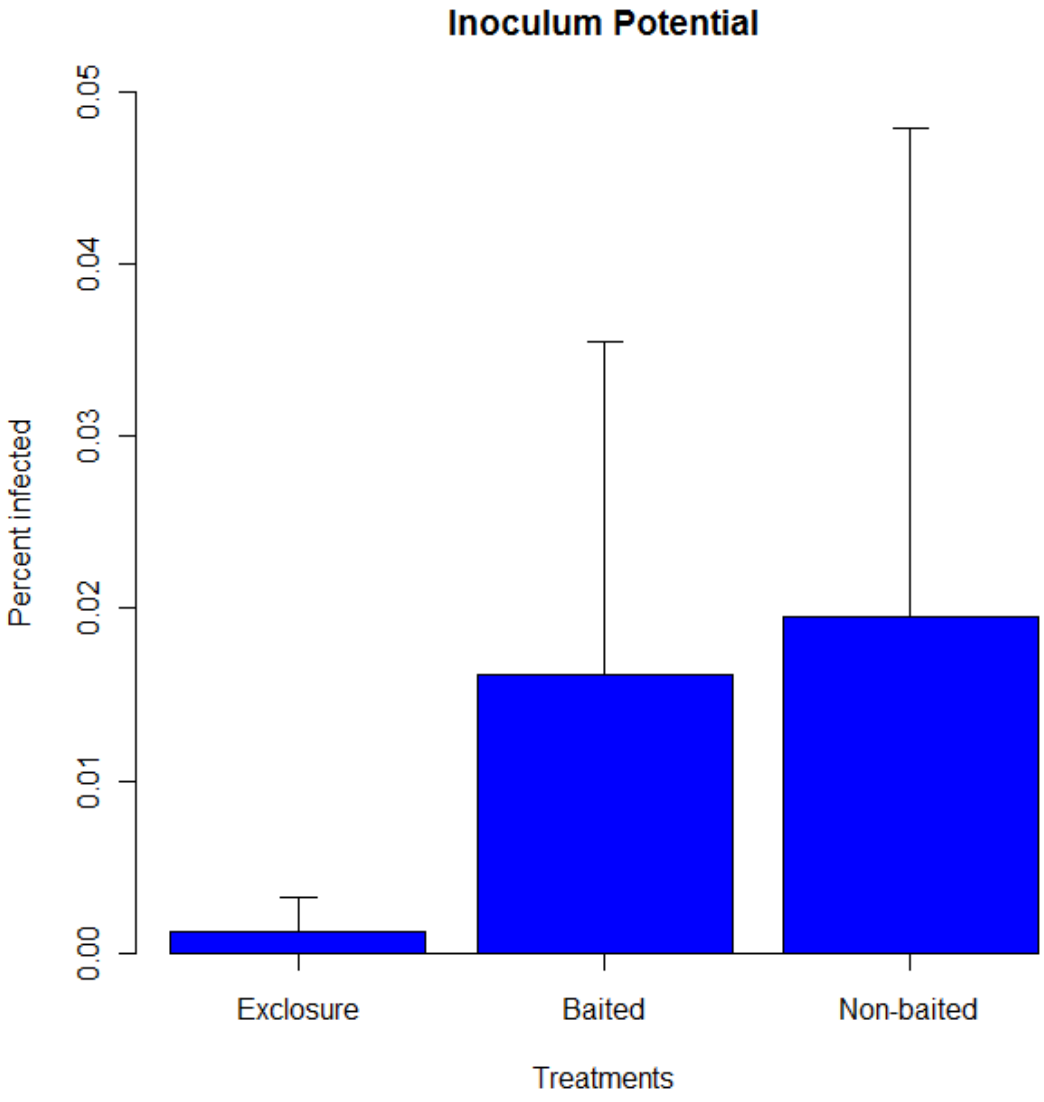
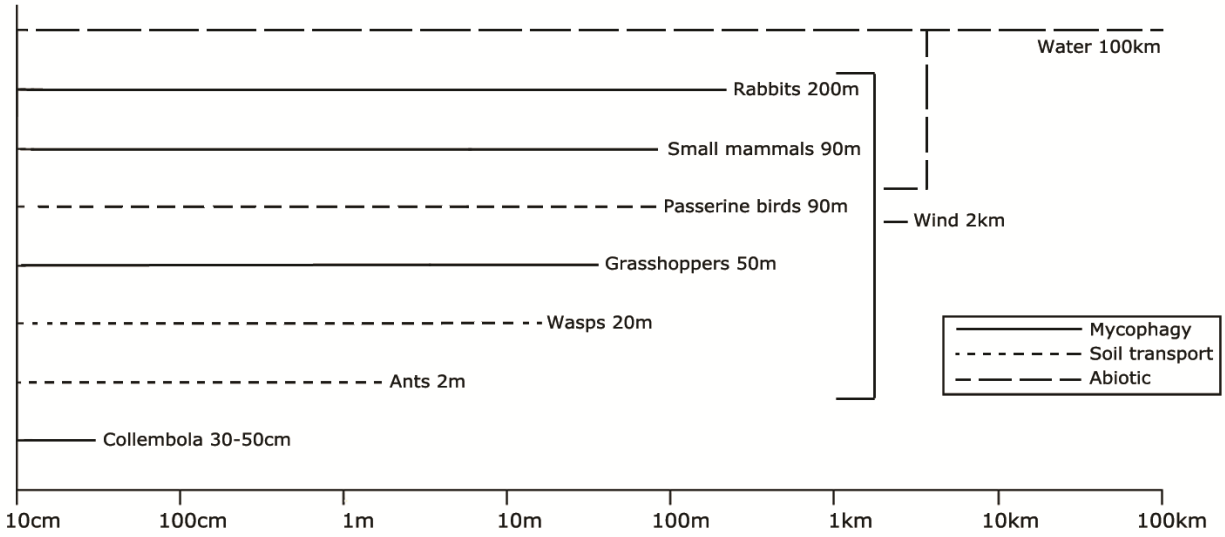


Figure 6.-Distances over which biotic and abiotic vectors transport arbuscular mycorrhizal fungi spores and hyphae. Animals may consume fungi (mycophagy) or transport soil containing fungi when constructing nests. Spores brought to the surface may then be dispersed by wind or water, or water may directly remove spores from the soil during floods.



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Zaharick, John G., and Harald Beck. 2012. An experimental test of small mammal dispersal of mycorrhizal fungi. Poster Presentation. Towson University Student Research and Scholarship Expo. Towson, Maryland.

Zaharick, John G., and Harald Beck. 2011. Comparing the influence of small mammal & wind activities on mycorrhizal recovery from a fungicide treatment. Poster Presentation. The Wildlife Society-Maryland and Delaware Chapter. Frostburg, Maryland.

Zaharick, John, and Howard P. Whidden. 2007. Assessment of the Subspecies Status of the Kittatinny Red-Backed Vole (*Clethrionomys gapperi rupicola*). Oral Presentation. Pennsylvania Academy of Science. Monroeville, Pennsylvania.

GRANTS AND AWARDS:

2012 Sigma Xi Grant-in-Aid of Research $500

2012-Fall Towson University Graduate Student Association research grant $500

2011-Fall Towson University Graduate Student Association research grant $300

2011-Spring Towson University Graduate Student Association research grant $300

TECHNICAL AND OTHER SKILLS:

Knowledge of hypothesis testing and information theoretic statistics and study design

Experience with programs: R, JMP, ArcGIS, Microsoft Office

Able to work independently in both office and field environments

Experience trapping, handling, and tagging small mammals