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Family Ties and Plant Invasions: Do Closely Related Native and Exotic Fern Species Differ in Mycorrhizal Colonization?

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FAMILY TIES AND PLANT INVASIONS: DO CLOSELY RELATED NATIVE AND EXOTIC FERN SPECIES DIFFER IN MYCORRHIZAL COLONIZATION?

By

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Although invasive plant species are known to decrease biodiversity and adversely affect native plant communities, factors that contribute to invasiveness are still poorly understood. Arbuscular mycorrhizas (AM) are an important biotic factor in many ecosystems, but evidence conflicts regarding their effects on invasive plant success. Nine species from four confamilial groups of native and exotic ferns in southern Florida were examined to determine their extent of mycorrhizal colonization. The mycorrhizal status of three species **(***Pteris bahamensis, Thelypteris dentata,* and *Thelypteris kunthii*) was determined for the first time. Significant differences in AM colonization were found among confamilial groups. No significant differences were found in the level of AM colonization between closely related native and exotic species, which suggests that evolutionary relationships better predict the level of AM colonization than whether a species is native or exotic. These findings also demonstrate that the exotic species tested were able to form relationships with AM fungi outside their native ranges.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter One: Introduction

Biological invasions by exotic plants can adversely affect ecosystems and cause major ecological damage (Adams et al. 2011; Mack et al. 2000; Pimental et al. 2000, Schmitz et al. 1997). The ecosystem impacts of exotic plants can be varied and complex; moreover, the nature and extent of these impacts may not be apparent for some time (Simberloff 2011; Daehler 2003; Ehrenfeld 2003; Pimental et al. 2000; Schmitz et al. 1997). The unpredictable behavior of exotic species once they enter a new habitat only serves to emphasize the importance of understanding what factors allow exotic species to be successful in new environments.

Biological Invasion Research

Although an abundance of research on biological invasions has been performed, how exotic plant species successfully establish and ultimately become invasive is still equivocal (Ahern et al. 2010; Kolar and Lodge 2001; Mack et al. 2000). Some studies have examined biological traits in hopes of finding a set of predictors for which species are likely to become invaders, but no overall picture of the "perfect invader" has yet emerged (Lloret et al. 2005; Goodwin et al. 1999; Crawley et al. 1996; Rejmanek and Richardson 1996). A similar approach examines characteristics of ecosystems to determine whether factors such as high species diversity or low anthropogenic disturbance can protect against biological invasions (Heger and Trepl 2003; Levine 2000; Levine and D'Antonio 1999). While it has been surmised that some ecosystems have natural resistance to invasion based on these types of factors, it has not been possible to verify such resistance experimentally (Heger and Trepl 2003) and empirical studies have provided conflicting evidence (Levine and D'Antonio 1999).

Because neither the direct examination of the biological traits of successful invaders nor of commonalities among invaded ecosystems has yielded unambiguous predictions of biological invasions, examining feedbacks between plants and ecosystems may be more realistic and more informative than previous approaches. One hypothesis (resource hypothesis) suggests that a sudden increase in the availability of resources in a habitat can lead to a competitive advantage for an exotic species and can allow it to establish more successfully or to spread if already present in the habitat (Blumenthal 2005; Davis et al. 2000). The success of the exotic plants in this scenario depends on their ability to utilize the excess of nutrients that become available and compete with native plants for these resources.

A second hypothesis, the enemy release hypothesis, is based on studies that suggest plant species outside their native range may escape from enemies such as soil pathogens or phytophagous insects and therefore have fewer natural constraints than native species (Blumenthal 2005; Mitchell and Power 2003; Keane and Crawley 2002; Klironomos 2002). The competitive advantage derived from enemy release can allow exotic plants to spread through an area without being inhibited by the same factors that affect native plant species. In conjunction, these two mechanisms (increased resource availability and enemy release) could synergistically increase the ability of an exotic species to invade an area (Blumenthal 2005), multiplicatively contributing to its competitive advantage in that area.

Arbuscular Mycorrhizas as a factor in biological invasions

Given that these two hypotheses for explaining how exotic plants are able to become invasive include interactions between plants and soil (resource hypothesis through nutrient uptake and enemy release hypothesis through interactions with soil pathogens or parasites), arbuscular mycorrhizas may be an important factor to consider for understanding the complex issue of biological invasions. Arbuscular mycorrhizas (AM) are mutually beneficial associations between the roots of plants and soil fungi in the phylum Glomeromycota. These mutualistic associations have been found in approximately 80% of the terrestrial plant species that have been examined, and they facilitate absorption of water and key mineral nutrients, particularly phosphorous and nitrogen (Smith and Smith 2011). If resource availability is a contributing factor in biological invasions (Davis et al. 2000), then AM could play an important role in the ability of a plant species to acquire available resources (e.g., soil nutrients and/or water).

In addition, unlike generally host-specific pathogenic microbes (Callaway et al. 2004), mycorrhizal fungi are not host-specific and can form mutualisms with a wide range of plant hosts (Newsham et al. 1995). Previous studies have demonstrated that invasive plant species can derive benefits from associations with indigenous mycorrhizal fungi. For example, Shah and Reshi (2007) found that an invasive herbaceous species (*Anthemis cotula*) grown with AM fungi present experienced favorable effects on both growth (increased stem length and shoot biomass) and reproduction (number of inflorescences and number of achenes) versus growth in AM free conditions. This exotic species (*A. cotula*) was also simultaneously experiencing release from herbivorous insects while experiencing favorable effects from its mutualism with mycorrhizal fungi

(Shah and Reshi 2007). Therefore, an exotic species might not only escape from its enemies, but might also concurrently benefit from the presence of AM leading to increased success (Shah and Reshi 2007; Callaway et al. 2004; Mitchell and Power 2003; Klironomos 2002).

Such potential benefit, however, depends on the species' capacity to respond positively to AM fungi (Janos 2007). Because many invasive plants are known to be nonmycorrhizal (i.e., do not form mutualisms with AM), determining whether an exotic species can form AM is especially pertinent (Pringle et al. 2009).

Study Area

The state of Florida ranks second only to Hawaii in the amount of ecosystem damage that has been caused by invasive plant species (Pemberton and Liu 2009; Schmitz and Brown 1994). Some of the factors, such as a subtropical climate, that make Florida's flora particularly diverse also provide favorable conditions for invasions by exotic plants from similar climates across the globe (Adams et al. 2011; Schmitz et al. 1997).

Florida has the highest fern diversity of any state with the exception of Hawaii, and many native fern species currently are threatened or endangered (Nelson 2000; Wunderlin and Hansen 2000; Small 1931). The Florida Exotic Pest Plant Council (FLEPPC) has designated six exotic fern species (three of which are included in this study) as "Category One" invasive plants, capable of "altering native plant communities by displacing native species, changing community structures or ecological functions, or hybridizing with natives" (FLEPPC 2011). The threat to native ferns from plant invasions therefore is of major ecological concern in this region.

In this study, by comparing AM colonization between confamilial native and exotic fern species, I explored the potential for either the presence or absence of AM to influence plant invasion. Within the southern Florida geographical area of my study, neither the presence nor absence of mycorrhizas previously has been reported for any of the nine fern species that I examined. I determined if the exotic species formed AM with indigenous fungi and how their extent of root colonization compared to that of native fern species in the same habitats.

Chapter Two: Methods

Study Species

I examined fern species in four families (Table 1) for evidence of mycorrhizal colonization to determine whether each fern species was mycorrhizal and to measure the extent of root length colonized by arbuscular mycorrhizal fungi. Of the four families examined, three contained congeneric native and exotic species, while the Polypodiaceae family contained native and exotic species with similar morphology and growth habit (*Phlebodium aureum* and *Phymatosorus scolopendria)* because no congeneric exotic species is naturalized in the study area.

Sample Collection

Root samples from twenty individual plants of each of the nine species were collected between May and November 2011. Wet season samples were collected between May 23, 2011 and June 19, 2011 while dry season samples were collected between September 9, 2011 and November 14, 2011. Collections were made at 34 sites across Miami-Dade, Broward, Martin, and Palm Beach Counties. Within each species, samples were collected from plants growing at least 20 meters apart and an effort was made to sample from as many different substrates (epiphytic, epilithic and terrestrial) and habitat types as possible. A total of 10 cm length of fine roots was collected from each individual plant.

To gain a representative measure of the plant's overall mycorrhizal colonization, roots were sampled from different sides of the plant's root system. Root samples were mechanically cleaned of soil and debris at the time of collection and were placed in separate dry plastic vials. In a few cases where it was not possible to begin processing

root samples on the day of collection, root samples were stored in 50% EtOH and processing began within 5 days.

At the time of collection, the substrate was noted and categorized in one of three groups depending on the amount of soil contacting the roots and the observed soil composition. Samples categorized as "No Soil" had roots with little or no contact with soil and generally were either epiphytes or were epilithic plants growing directly on bare rock surfaces. Samples categorized as "Intermediate" had roots with moderate soil contact and generally were growing in crevices between rocks, or in rocky soil. Samples categorized as "Soil" had all roots within the soil and contact with the soil was not interrupted. To ensure that each plant collected had reached reproductive maturity, an effort was made predominately to collect plants that demonstrated the ability to produce spores. Overall, 75% of samples were collected from plants that were producing spores or showed evidence of having recently produced spores at the time of collection.

Root Sample Preparation

A modified Phillips and Hayman (1970) method was used to clear and stain roots for observation of mycorrhizas (Fernandez et al. 2008). Roots were rinsed in cool water and each 10 cm sample was cut into 2 cm sections. Root sections were placed in 125 mL Erlenmeyer flasks, covered with approximately 75 mL of 10% KOH solution, and placed in an incubator at 60° C. After 12 hours, the samples were examined and, if necessary, the KOH solution was decanted, replaced with fresh solution, and the flasks were returned to the incubator. This process was repeated until roots were cleared. Cleared roots were rinsed in cool water and, if necessary, were bleached in 3% (v/v) H_2O_2 for 2-5 minutes. After clearing or bleaching, all root samples were acidified in 1N HCl at room

temperature for one minute. Acidified root samples were stained with Trypan Blue in acidic glycerol (31% v/v glycerol, 31% v/v lactic acid, 0.05% w/v Trypan Blue) for 6 hours at 60° C in an incubator. Root samples then were removed from the Trypan Blue stain solution and placed in acidic glycerol at room temperature.

Microscopy

For each root sample (representing one individual plant), 20 intersections were examined using a modified McGonigle magnified intersections method (McGonigle et al. 1990) along the full length of each of five 2 cm root sections at 400x magnification under a light microscope. Intersections were defined as the point on the root where the eyepiece crosshair was centered (McGonigle et al. 1990). During microscopy, the stage was moved approximately regular (but not measured) intervals so as to examine intersections across the entire length of the sample. Intersections were sufficiently distanced from one another to avoid tallying the same fungal structure more than once. Observations at intersections therefore were independent, although neither randomly nor uniformly spaced. For each species, root samples from 20 individuals were examined for a total of 2000 intersections per species. Slides were identified only by sample number in order to prevent bias during microscopic examination. Each intersection was scored for arbuscules (Figure 1A), vesicles (Figure 1B), internal hyphae, and no AM fungus structures present. Arbuscules and vesicles were tallied only when distinct hyphal attachments were observed, and internal hyphae were tallied exclusively in the absence of arbuscules and vesicles such that total colonization is the sum of the three AM categories. No external hyphae or non-glomeromycotan regularly septate hyphae (Figure 1C) were tallied.

During microscopic examination it was also noted whether the colonization pattern was *Arum*- type (intercellular hyphae from which branch intracellular arbuscules) or *Paris*- type (intracellular hyphae, coils, and arbusculate coils) (Dickson 2004).

Data Analysis

Three separate three-way analysis of variance (ANOVA) models, each using a different way of classifying the ferns, were used to examine AM colonization in the roots of ferns with the number of positively scored intersections of each plant as the dependent variable. Because the number of positive intersections was used, no transformation of the data was necessary. The first model examined whether status (native or exotic) affects AM colonization; the second model examined family; and the third model examined species.

Because samples were collected in two groups separated by time, season was included as an independent variable in each statistical model to determine if there was an effect of season. Because mycorrhizal colonization can be influenced by mineral nutrient availability (Pringle et al. 2009; Cornwell et al. 2001) and samples were collected from different substrate types, substrate also was included as an independent variable in each model to determine if there was an effect of substrate type.

Within each model, all interactions between season, substrate, and the third variable (fern classification) were examined. To test for pairwise differences when a factor was found to be significant, Tukey's HSD test was employed.

Homogeneity of variances was not rejected by the Brown-Forsythe test for any of the three models, but Levene's test did indicate lack of homogeneity for the model examining family. Levene's test is very sensitive to non-normality, so this result for the

model examining family likely is attributable to the small number of samples for many of the 24 combinations of factors. Tests were judged significant if $P < 0.05$. JMP statistical software (JMP Version 9.0, SAS Institute) was used for all data analyses.

Chapter Three: Results

All species in this study, whether native or exotic, were found to be mycorrhizal based on the presence of arbuscules and/or vesicles in at least one of the 20 samples examined (Table 2). No species was considered to be mycorrhizal based solely on the presence of intraradical hyphae. Due to the ephemeral nature of arbuscules, and the fact that arbuscules were tallied only when a visible hyphal attachment was observed, the number of arbuscules recorded is a conservative estimate. For three species (*Nephrolepis brownii, N. cordifolia* and *N. exaltata*), individual plant samples were found that were entirely free of arbuscules, vesicles, and intraradical hyphae. For the other six species, every sample was found to have at least one intersection with evidence of mycorrhizal colonization based on observations of arbuscules, vesicles, and/or intraradical hyphae (although some samples had only intraradical hyphae). For all nine species there was similar variation among samples in the relative number of observed arbuscules, vesicles, and intraradical hyphae.

Mycorrhizal colonization type

No species fell exactly within either *Arum*-type or *Paris*-type, so the pattern of hyphal colonization observed was invariably characterized as "intermediate" for every species. This most closely fits Dickson's (2004) category "Intermediate 2" because hyphae ran intracellularly, but coils were not present although arbuscules were.

Effect of status on mycorrhizal colonization

Status (if a species is native or exotic) was not found to significantly affect AM colonization (Table 3; Figure 2). Within this model, neither season, substrate, nor any of their interactions were found to have a significant effect on mycorrhizal colonization (Table 3).

Effect of family on mycorrhizal colonization

Family was found to significantly affect mycorrhizal colonization (P= <0.001; Table 4). Within this model, neither season nor substrate had a significant effect as main factors, but their interaction (season x substrate) was found to be significant (P= 0.002; Table 4). The significance of this interaction was found to arise from the interaction of wet season and soil substrate. This particular combination yielded higher AM colonization in some samples compared to other combinations of season and substrate. In three of the species examined (*Nephrolepis brownii, Pteris vittata, and Thelypteris kunthii*), the sample with the highest percent root length colonized was collected during the wet season from a soil substrate. Because this interaction does not involve family, it has no bearing on the significance of the main effect of family. This model was the most strongly predictive (R^2 Adj=0.500344) of the three models.

Tukey's HSD test revealed that some families differed significantly from others (Figure 2). Pteridaceae and Thelypteridaceae did not differ significantly from each other but did differ significantly from Lomariopsidaceae and Polypodiaceae which each differed significantly from all other families.

Effect of species on mycorrhizal colonization

Species was found to significantly affect mycorrhizal colonization (P=0.002), but because some interactions were not observed this model lost degrees of freedom and is not tabled. This model was also marginally less predictive (R^2 Adj=0.500338) than the model using family as the main factor.

Other root colonization

For seven of the nine fern species examined, root colonization by fungi other than AM fungi was observed. These other fungi were identified as non-AM by their uniform diameter, frequently and regularly septate hyphae, and by the presence of sporangia within root cells or spores not typical of AM fungi. In total, 24% of all 180 fern root samples were colonized by non-AM fungi, but the percentage of root length colonized by non-AM fungi was not quantified. For only two species, *Nephrolepis brownii* and *Nephrolepis cordifolia,* both of which are exotic species, was there no observed colonization by non-AM fungi.

Chapter Four: Discussion

In southern Florida, I found AM colonization in both native and exotic fern species within confamilial groups and wide variation in colonization among families. I found that the status of a species as native or exotic, however, did not significantly affect AM colonization (Table 3).

Although seasonal differences previously have been shown to affect the AM colonization of tropical trees (Torti et al. 1997), I found that the season of sample collection had no influence on overall AM colonization. It also is known that soil fertility, particularly the amount of available phosphorous, can affect AM colonization (Pringle et al. 2009; Cornwell et al. 2001). Soil fertility was not measured in this study, but because substrate type as defined in this study directly influences the nutrients available to a plant, it was used as a proxy for soil fertility. Type of substrate as a main effect, however, did not significantly affect AM colonization.

Evolutionary interpretation of results

Because neither season, substrate, nor status influenced AM colonization, the best predictor of colonization in my study is the family to which a particular species belongs (Figure 2). While this result was not expected, it is not entirely unprecedented. It previously has been theorized that evolution in pteridophytes is accompanied by a decrease in mycorrhizal dependence (Boullard 1979). Because Boullard's hypothesis (1979) relates to mycorrhizal dependence and not directly to amount of colonization, my data do not pertain precisely. Nevertheless, my results do suggest that evolutionary relationships play a role in influencing AM colonization of fern species.

According to recent molecular phylogenetic analyses (Smith et al. 2006), Lomariopsidaceae and Polypodiaceae are the most closely related and the most diverged of all the families sampled in this study, and these two families had the two lowest average levels of colonization (Figure 2). Thelypteridaceae is the next most diverged family from among those sampled, and it has the next lowest average colonization, while Pteridaceae, which is the most basal family among those sampled, has the highest average mycorrhizal colonization. Therefore, phylogenetic relationships (Smith et al. 2006) correlate well with the average amounts of colonization observed among the four fern families that I examined (Fig. 2, Table 2).

Congeneric species hypothesis

Much debate exists over whether exotic species are more likely or less likely to naturalize in an area where native congeners are found. Some studies support the theory that the presence of a native congener makes it less likely that an exotic species will be able to successfully establish (Rejmanek 1998; Mack 1996), while other studies contradict these findings (Lambdon and Hulme 2006; Daehler 2001). Because AM can affect the success of exotic species (Shah and Reshi 2007; Callaway et al. 2004; Mitchell and Power 2003; Klironomos 2002), knowing if exotic species are colonized by mycorrhizal fungi in an area could help predict their potential success in that area.

My study found no significant differences in AM colonization between confamilial native and exotic fern species, which indicates that the exotic species are responding positively to AM in a similar way to their close native relatives.

In addition, exotic species in my study were frequently growing within half a meter of their close native relatives, an observation inconsistent with the theory that the presence of a native congener makes it more difficult for an exotic species to establish.

Previous research on AM in the study species

Of the nine species in this study, six previously have been examined for mycorrhizas (Kessler et al. 2010; Zhang et al. 2004; Zhao 2000; Moteetee et al. 1996; Gemma et al. 1992). Of those six species, *Nephrolepis cordifolia, Nephrolepis exaltata,* and *Nephrolepis brownii* all were found to be mycorrhizal in Hawaii, similar to my findings, based on the presence of arbuscules in the roots of the samples examined. For *Nephrolepis cordifolia,* 3 out 3 samples examined were determined to be mycorrhizal, for *Nephrolepis exaltata* 11 out of 11 were mycorrhizal, and for *Nephrolepis brownii* 15 out of 26 samples were mycorrhizal (Gemma et al. 1992). *Phlebodium aureum* was found to be non-mycorrhizal, in contrast to my observations for this species, though only one individual plant was examined (Gemma et al. 1992). *Phymatosorus scolopendria* was found to be non-mycorrhizal in Hawaii in both samples examined (Gemma et al. 1992) and non-mycorrhizal on the island of La Réunion in both samples examined (Kessler et al. 2010) in contrast to my findings. The remaining species, *Pteris vittata* was found to be mycorrhizal in Hawaii in one sample examined (Gemma et al. 1992), in Lesotho in two samples examined (Moteetee et al. 1996), and on La Réunion in one sample examined (Kessler et al. 2010) similar to my findings. In contrast, this species was found to be non-mycorrhizal in three samples from Yunnan, southwest China (Zhao 2000), and showed evidence of vesicles but no arbuscules in two samples examined in Dujiangyan, southwest China **(**Zhang et al. 2004). I describe the mycorrhizal status of the remaining

three fern species *Pteris bahamensis, Thelypteris dentata,* and *Thelypteris kunthii* for the first time in this study.

In contrast to these previous studies, my study sampled more individual plants as well as more root intersections per sample, resulting in greater length of root with independent tallies of AM examined per species. This allowed me to quantify AM colonization with a higher degree of confidence and consistency.

Additional examinations of all these species are needed to ascertain if there are any general patterns linking their mycorrhizal status to whether they are indigenous to an area.

Conclusions

Although no statistically significant differences in AM colonization were found between native and exotic fern species, significant differences were found between some families. These findings imply that exotic ferns can be as successful in forming relationships with mycorrhizal fungi as closely related native species growing in the same habitats. Further investigation could determine whether native and exotic species have similar dependence on these AM relationships.

Because a plant species' degree of dependence on mycorrhizas cannot be inferred unambiguously from the extent to which it is colonized by mycorrhizal fungi, (Janos 2007), how the observed amounts of colonization may influence a species' success is still unresolved.

Much literature suggests that arbuscular mycorrhizas are a complex and important biotic factor influencing plant communities, so failure to include them in studies of biological invasions is a large oversight. The findings of this study offer insight regarding the incidence of AM among ferns and help to rectify the knowledge gap in this area of invasion biology.

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Table 1 Species of ferns examined

Family	Species	Status
Lomariopsidaceae	*Nephrolepis cordifolia* (L.) Presl	Exotic[a]
Lomariopsidaceae	*Nephrolepis exaltata* (L.) Schott	Native
Lomariopsidaceae	*Nephrolepis brownii* (Desv.) Hovenkamp & Miyam.	Exotic[a]
Polypodiaceae	*Phlebodium aureum* (L.) J. Sm.	Native
Polypodiaceae	*Phymatosorus scolopendria* (Burm. f.) Pic. Serm.	Exotic[a]
Pteridaceae	*Pteris bahamensis* (J. Agardh) Fée	Native
Pteridaceae	*Pteris vittata* (L.)	Exotic
Thelypteridaceae	*Thelypteris kunthii* (Desv.) Morton	Native
Thelypteridaceae	*Thelypteris dentata* (Forssk.) E.P. St. John	Exotic

[a]Status: Listed as invasive on the Florida Exotic Pest Plant Council 2011 Invasive Plant List

Table 2 Mycorrhizal structures observed per species

Host Species	Arbuscules	Vesicles	Intraradical Hyphae	AM[a]	Myco. freq[b]
Nephrolepis cordifolia	2	2	133	137	10%
Nephrolepis exaltata	3	3	161	167	15%
Nephrolepis brownii	0	6	232	238	25%
Phlebodium aureum	0	19	554	573	45%
Phymatosorus scolopendria	0	11	581	592	30%
Pteris bahamensis	11	36	920	967	80%
Pteris vittata	13	67	951	1031	80%
Thelypteris kunthii	0	42	757	799	90%
Thelypteris dentata	1	26	793	820	65%

[a]AM: total intersections with arbuscules, vesicles, and intraradical hyphae out of 2000 intersections examined per species
[b]Mycorrhiza frequency: The percentage of plants with arbuscules and/or vesicles present among 20 individuals of each host species

Table 3. ANOVA for the effects of status (i.e., native vs. exotic), season, substrate type, and their interactions on total AM colonization.

Effects		Root Length Colonized		
	Df	Sum of Squares	F	P
Status	1	383.03	0.75	0.387
Season	1	365.52	0.72	0.398
Substrate	2	1168.96	1.15	0.320
Status x Season	1	143.06	0.28	0.597
Status x Substrate	2	20.72	0.02	0.980
Season x Substrate	2	570.33	0.56	0.572
Status x Season x Substrate	2	476.18	0.47	0.627
Error	168	85582.24		
Total	179	89046.06		

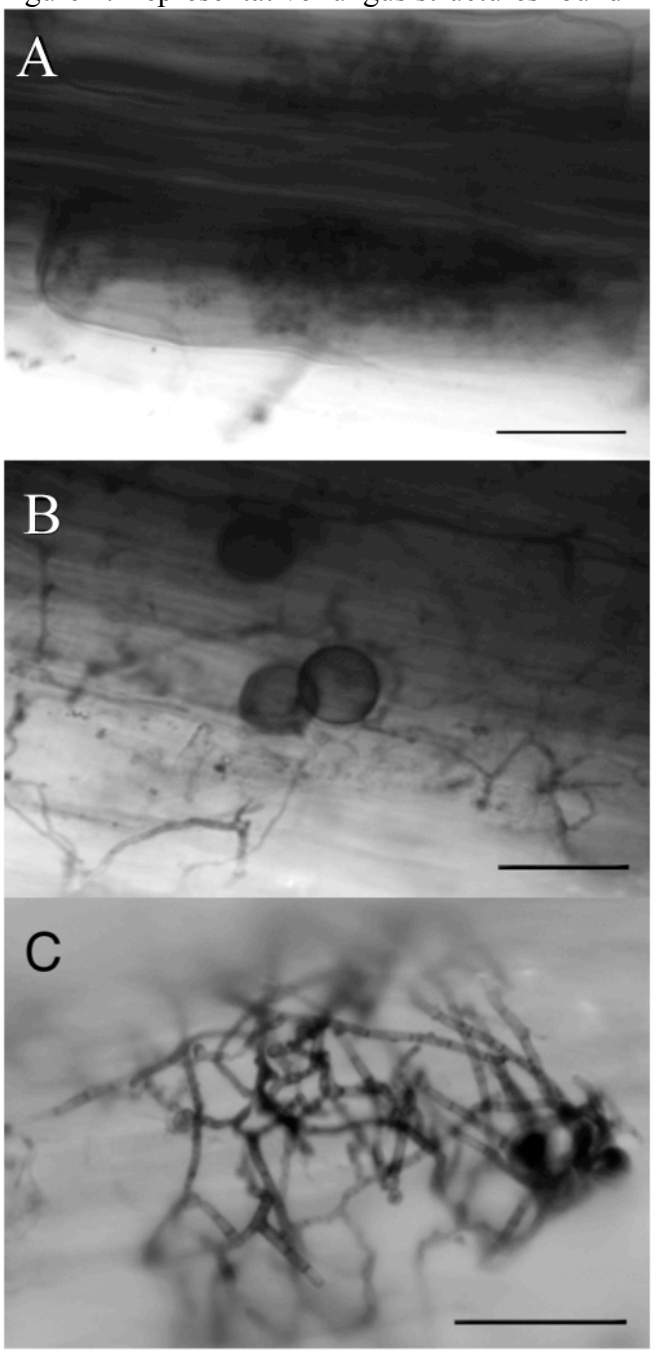
R^2 Adj = -0.024

Table 4. ANOVA for the effects of family, season, substrate type, and their interactions on total AM colonization.

Effects		Root length colonized		
	Df	Sum of Squares	F	P
Family	3	41543.71	55.71	**<0.0001**
Season	1	59.54	0.24	0.625
Substrate	2	23.65	0.05	0.953
Family x Season	3	1450.14	1.94	0.125
Family x Substrate	6	510.88	0.34	0.913
Season x Substrate	2	3179.87	6.40	**<0.002**
Family x Season x Substrate	6	2861.05	1.92	0.081
Error	156	38775.53		
Total	179	89046.06		

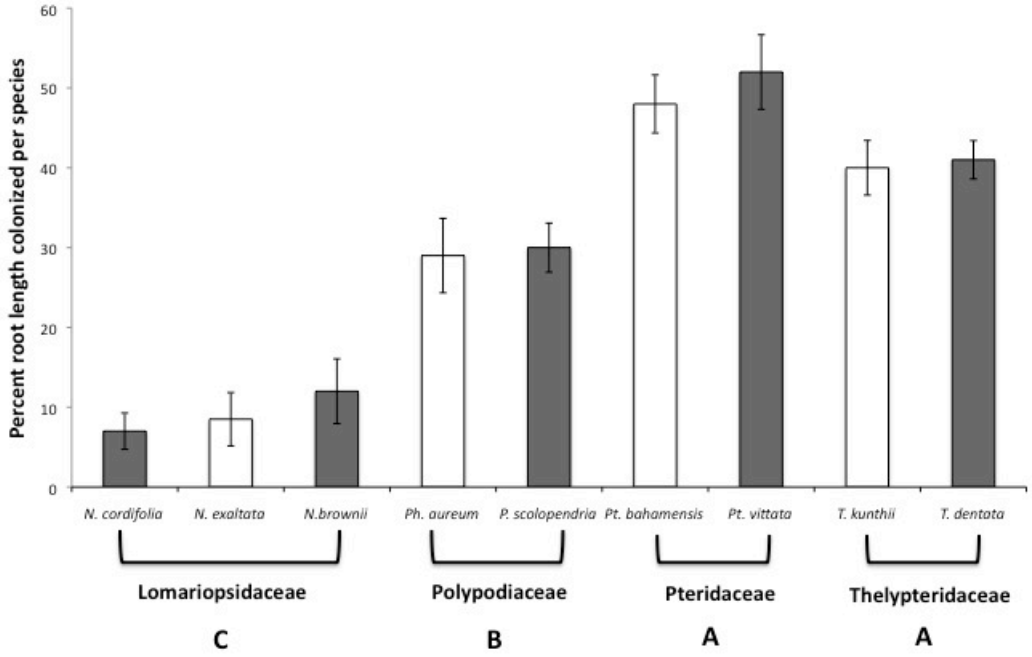
R^2 Adj = 0.500
Bold indicates a significant effect

Figure 1: Representative fungus structures found in fern roots



(A) Arbuscules within cortical cells (plane of focus at wall of lower cell) of *Pteris bahamensis*.
(B) Nearly spherical vesicles in root of *Thelypteris dentata*.
(C) Non-AM, regularly-septate hyphae in *Phymatosorus scolopendria*.
Scale bar is 50 µm in A-C.

Figure 2: Mean percentage root length (+/- SE) internally colonized by all AM fungus structures (arbuscules, vesicles, and hyphae) for all species examined



Note: Shaded bars represent exotic species while open bars represent native species.
Families represented by the same letter do not differ significantly (Tukey HSD test).