MYCOTROPHIC STRATEGY OF 13 COMMON NEOTROPICAL TREES AND SHRUBS

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MYSTER RW, LEBRON L, LOAYZA ABP & ZIMMERMAN JK. 2013. Mycotrophic strategy of 13 common neotropical trees and shrubs. We conducted a greenhouse experiment using common Puerto Rican trees and shrubs that span the spectrum of neotropic life histories. Our working hypothesis was that species had a higher colonisation rate of arbuscular mycorrhizal fungi (AMF) as they established further and further after a disturbance (quantified as increasing seed size). Results suggested that (1) *Cecropia schreberiana* and *Schefflera morototoni* were weakly-facultative mycorrhizal, (2) *Casearia arborea*, *Inga laurina* and *Guarea guidonia* were strongly-facultative mycorrhizal and (3) *Piper glabrescens, Tabebuia heterophylla, Palicourea riparia, Buchenaria capitata* and *Dacryodes excelsa* were obligately mycorrhizal with (4) *Psychotria berteriana, Prestoea montana* and *Manilkara bidentata* also obligate but at a reduced level. In general, these species were adapted to low inorganic phosphorus, colonised well with AMF and agreed with our working hypothesis; however, three shrub species (*Piper, Palicourea, Psychotria*) did not. Finally, we also found that shade tolerance of the test species corresponded with the AMF results better than their wood density or drought tolerance.

Keywords: AM fungus, phosphorus, Puerto Rico, LTER

MYSTER RW, LEBRON L, LOAYZA ABP & ZIMMERMAN JK. 2013. Strategi mikotrofik 13 pokok dan pokok renek neotropika biasa. Kami menjalankan eksperimen rumah kaca menggunakan pokok dan pokok renek yang biasa ditemui di Puerto Rico dan wujud merentasi spektrum riwayat hidup neotropika. Hipotesis kami ialah spesies mempunyai kadar pengkolonian kulat mikoriza arbuskel yang lebih tinggi (AMF) apabila ia tumbuh semakin jauh akibat gangguan (yang disukat sebagai peningkatan saiz biji benih). Keputusan mencadangkan bahawa (1) *Cecropia schreberiana* dan *Schefflera morototoni* merupakan mikoriza fakultatif yang lemah, (2) *Casearia arborea, Inga laurina* dan *Guarea guidonia* merupakan mikoriza fakultatif kuat, (3) *Piper glabrescens, Tabebuia heterophylla, Palicourea riparia, Buchenaria capitata* dan *Dacryodes excelsa* merupakan mikoriza obligat dan (4) *Psychotria berteriana, Prestoea montana* serta *Manilkara bidentata* merupakan obligat juga tetapi pada tahap yang lebih rendah. Pada umumnya, kesemua spesies ini telah mengadaptasi untuk hidup dalam kandungan fosforus tak organik yang rendah dan mengkoloni dengan baik dengan AMF. Ini bertepatan dengan hipotesis kami walaupun tiga (*Piper, Palicourea, Psychotria*) spesies pokok renek terkecuali. Akhirnya, kami juga dapati ketahanan spesies ujian terhadap teduhan lebih sejajar dengan keputusan AMF berbanding dengan ketumpatan kayu atau ketahanan terhadap kemarau.

INTRODUCTION

The roots of the majority of vascular plant species form symbiotic associations with arbuscular mycorrhizal fungi (AMF), improving their survival and growth due to enhanced uptake of soil nutrients (up to 80% phosphorus (P) and 25% nitrogen (N) required by plants), improved water relations and reduced pathogenic infections (Whipps 2004). These effects may depend, however, on soil nutrient availability (Zangaro et al. 2003) where AMF can cause growth depressions under high nutrient supply (Gehring 2003, Janos 2007). AMF may also preclude the formation of N-fixing nodules for some legumes on P-poor soils while increasing nodulation and N-fixation rates in most others (Mabberley 1992). In addition, AMF may affect nodulation through competition both directly for host carbon and indirectly through resources that AMF and nodulation supply independently to the host (Cluett & Boucher 1983). An AMF association increases the competitive ability of plants, especially for late-successional obligate mycotrophic species. AMF has both positive and negative effects for less dominant plants in communities (Hartnett & Wilson 1999). Indeed, AMF hyphae may connect neighbouring plants and thus influence plant richness and change plant distribution and composition (Myster & Fernandez 1995, Myster 2007). Finally, knowledge about the ability of plant species to form AMF associations can be essential for reforestation and restoration success.

Mycorrhizae association degree, or mycotrophic strategy, varies along a symbiotic continuum from obligately mycotrophic species that must have the association to survive (e.g. *Andropogon gerardii*) to facultatively mycotrophic species that may or may not take up the association depending on soil conditions such as P availability (e.g. *Elymus canadensis*), and finally to non-mycotrophic species that never form the association (e.g. *Myrsine australis*) under nutrient levels normally encountered. Although it is generally thought that AMF strategies and soil nutrient trade-offs are important in determining plant distribution, abundance and composition (Lovelock et al. 2003, Kottke et. al. 2004), little is known about AMF strategies of individual species and the environmental conditions under which species take up or do not take up the association. In particular, information is scarce in the species-rich communities found in tropical rainforests. However, data that is available show the importance of AMF for tree growth (Kiers et. al. 2000).

Therefore, in order to better understand interactions between AMF and P, and the resulting AMF strategy of individual neotropical tree and shrub species, we conducted a greenhouse experiment using common woody species found in Puerto Rico of genera common elsewhere in the neotropics (Myster 2007). These 13 trees and shrubs span the spectrum of life histories found in tropical forests from early successional pioneer species to subdominant understorey species, dominant canopy species and emergent species. Our working hypothesis was that tropical trees and shrubs had a higher rate of colonisation of AMF as they established later and later after a disturbance as poorly mobile ions such as phosphate become less and less available. Although the actual per cent root colonisation is measured, seed size is used to motivate the working hypothesis because (1) studies have shown a relationship between seed size and AMF dependency, (2) trees with larger seeds establish later in succession, and (3) seed size is known to correlate with other aspects of tropical tree life histories such as seed dispersal vector, wood density, growth rate, understorey survival probability and shade tolerance. In general, seed size and other seed characteristics are essential to tropical tree life histories because they determine where and how establishment can take place (Grubb 1977). Finally, other trait data of these 13 trees and shrub woody density, shade tolerance and drought tolerance were compared with the degree of mycotrophy as a first attempt to generate potential patterns of woody neotropical life histories.

MATERIALS AND METHODS

Starting August 1997, seedlings were collected from each of these 13 woody species, here listed in order of increasing average seed mass (Francis & Rodriguez 1993): *Piper glabrescens, Cecropia schreberiana, Casearia arborea, Tabebuia heterophylla, Schefflera morototoni, Palicourea riparia, Psychotria berteriana, Inga laurina, Guarea guidonia, Prestoea montana, Buchenaria capitata, Manilkara bidentata* and *Dacryodes excelsa.* Ten of the species were trees and three (*P. glabrescens, P. riparia, P. berteriana*) were shrubs. All tree seedlings were collected in the Luquillo Experimental Forest (LUQ) of Puerto Rico, USA, a Long-Term Ecological Research (LTER) site of the National Science Foundation (http://luq.lternet.edu). Seedlings were transplanted into 1-L pots filled with steamed soil mix media and allowed to grow until 10 cm tall before treatments were applied. All experiments took place in a greenhouse.

After three months growth, 20 seedlings of each species with similar height were chosen for the experiment and transferred to 18.9-L pots filled with steamed soil mix media. A complete randomised block design experiment was set up for each tree species with five replicates of four different treatments: (1) control plants without addition of AMF but with low P addition, (2) plants with AMF added and with low P addition, (3) plants with high P addition but with no addition of AMF, and (4) plants with high P addition and with AMF added. Low P was realised with 0.58 g m^{-2} triple-super phosphate (P_2O_5) added once at the start of the experiment and high P with 0.58 g m^{-2} P_2O_5 added at the start, again after three months, and again after six months. AMF treatments were sterilised by steaming the soil to kill all AMF spores (no addition of AMF) and then adding 50 g of AMF-infected *Guarea* sp. root fragments collected under a single *Guarea* tree (addition of AMF). The AMF was known to infect large numbers of tree species in Puerto Rico and all 13 of the test tree species (Lodge 1987, Li et. al. 2006). In order to determine the P treatment levels, a preliminary experiment was performed on successional soil where most of these species were found by adding P (in the form of P_2O_5) to soil samples until there was a saturation of the fixation sites. This occurred at 0.58 g m^{-2} of pot surface area with a large increase of extractable P using inductively coupled plasma spectroscopy after H_2O_2 and HNO_3 digestion (Luh-Huang & Schultz 1985).

Light levels in the greenhouse were approximately 85% of full sunlight or 40 mol m^{-2} total daily photosynthetic photon flux density. The temperature and relative humidity were monitored inside the greenhouse where a daily watering regime was maintained. Mean daily temperature was 36 °C with a range of 25–40 °C and mean humidity was 80% with a daytime maximum of 55% and a nighttime maximum of 95%. Monthly environmental variation within the greenhouse was small due to the tropical location.

The greenhouse could only accommodate four species at a time, so the 13 study species were divided into three groups of four and one group of one, with the first group planted on 1 October 1997 and harvested 8 months later when a fine root sample was taken for analysis from each individual seedling. The second group was started immediately after the first one was harvested with the same procedures and this continued until all 13 species were investigated. For each group, fine roots were first cleared with alternating hot KOH and cold H_2O with NH_4OH and HCL. The roots were then acidified with five drops of HCL, stained with acid fuchsin and mounted on microscope slides with glycerin. The AMF density was estimated by placing the slide on a 5-mm grid and noting the proportion of roots intersecting the grid that were mycorrhizal (Lodge 1987, Li et. al. 2006, Myster 2006).

Treatment effects were investigated with a two-way (AMF, P) analysis of variance (ANOVA) using Wilks' lambda (SAS Version 5, 1985), taking the per cent of AMF colonisation as the response variable. Homogeneity of variances was checked in all cases before tests were done and normality was assured. Pots were arranged randomly in the greenhouse and rearranged every month. There were no significant block effects due to pot location within the greenhouse. In addition, the Ryan-Einot-Gabriel-Welsch multiple range test (SAS Version 5, 1985) was used to investigate significant differences between treatments. The sequential Bonferroni test (Rice 1989) was employed to investigate whether any significant effects should be viewed with suspicion. Finally, Spearman's rank correlation correspondence analysis (Myster 2007) was used to explore how the species ranked based on degree of mycotrophy compared with ranks based on other possible life-history traits.

RESULTS

All but two of the test species (*Cecropia, Schefflera*) showed significant effects of either AMF or P addition (Table 1). All other species had significant main effect of AMF addition, with three species (*Casearia, Inga, Guarea*) also showing significant main effect of P addition (Table 1). *Cecropia* had mean colonisation level of 29% (Figure 1b) and *Schefflera,* 33% (Figure 1e). The low level response of both of these species could represent a weakly-facultative mycotrophy strategy.

Casearia showed the largest increase in root colonisation after AMF addition. However, both treatments increased per cent root colonised with mean level of 35% (Figure 1c). Interestingly, *Inga* (Figure 1h) had per cent root colonised increased after AMF addition but decreased after high P addition, with a mean level of 22%. *Guarea* showed large increase in

Table 1 F statistic summary of the main effect of addition of arbusular mychorrizae fungi (AMF), phosphorus (P) and the interaction effects for the 13 test tree species

Species	AMF main effect	P main effect	AMF × P interaction effect
Piper glabrescens	7.25*	1.11	0.52
Cecropia schreberiana	1.58	0.33	0.32
Casearia arborea	80.4***	11.6**	1.65
Tabebuia heterophylla	6.43*	0.89	1.37
Schefflera morototoni	3.01	1.03	0.25
Palicourea riparia	4.06*	0.03	0.20
Psychotria berteriana	6.07*	0.33	2.14
Inga laurina	4.18*	4.49*	0.63
Guarea guidonia	57.7***	85.2***	0.12
Prestoea montana	10.95**	0.21	1.81
Buchenaria capitata	32.65***	0.75	0.82
Manilkara bidentata	3.42*	0.28	0.11
Dacryodes excelsa	22.24**	0.03	0.01

Results are sorted by increasing tree seed fresh mass; * = $0.01 < p < 0.05$, ** = $0.001 < p < 0.01$ and *** = $0.0001 < p < 0.001$; degree of freedom for all tests = 1

coverage after each treatment (Figure 1i) with a mean level of 44%. These responses represent stronger facultative mycotrophy strategy than those species presented previously, thus, tending towards a medium-facultative mycotrophy strategy (rarely takes up AMF), *Inga* more in the weak end of a strong strategy, *Casearia* in the middle/strong section of the facultative continuum and *Guarea* towards the strong section of the facultative continuum.

The species that had only a significant main effect of AMF addition could be divided into two groups. The first group showed large increase of per cent root colonised after addition of AMF. This included *Piper* (Figure 1a: mean 33%), *Tabebuia* (Figure 1d: 50%), *Palicourea* (Figure 1f: 36%), *Buchenaria* (Figure 1k: 31%) and *Dacryodes* (Figure 1m: 34%). The second group showed smaller increase of per cent colonisation after addition of AMF, which included *Psychotria* (Figure 1g: 29%), *Prestoea* (Figure 1j: 14%) and *Manilkara* (Figure 1l: 5%). Whereas these responses represent an obligately mycotrophy strategy, group one may be more obligate than group two. Finally, among the other three major known life-history strategy characteristics, seed size had significant rank correlation with the species order based on AMF responses (Table 2). Shade tolerance was also significant but wood density and drought tolerance were not.

DISCUSSION

Results agreed with the general finding that most tropical trees and shrubs formed AMF associations and many were obligately mycotrophic. In addition, results conformed well to expectations based on successional life-history status inferred from seed size, i.e. there was strong correspondence of increasing AMF colonisation with increasing seed mass (Kiers et. al. 2000) but did not agree with results reported by Zangaro et al. (2003). However, there were a few species that seemed to ‘jump out of line’: (1) *Piper* should have been weakly-facultative mycorrhizal with seed mass similar to *Cecropia* and *Schefflera* and (2) *Tabebuia, Palicourea* and *Psychotria* could be assumed to be more strongly-facultative with seed mass similar to *Casearia, Inga* and *Guarea.* Growth form or habit may be an extra consideration because all of the shrubs in this study are included among these species. Taken together, the results suggested that mycotrophic classes were not discrete but ranged over a continuum of responses such as other life-history traits (Poorter & Bongers 2006) and that tropical tree life histories might be complex and not easily put into categories (Lugo & Zimmerman 2002). It should be noted, however, that greenhouse studies may not always reflect plant responses in the

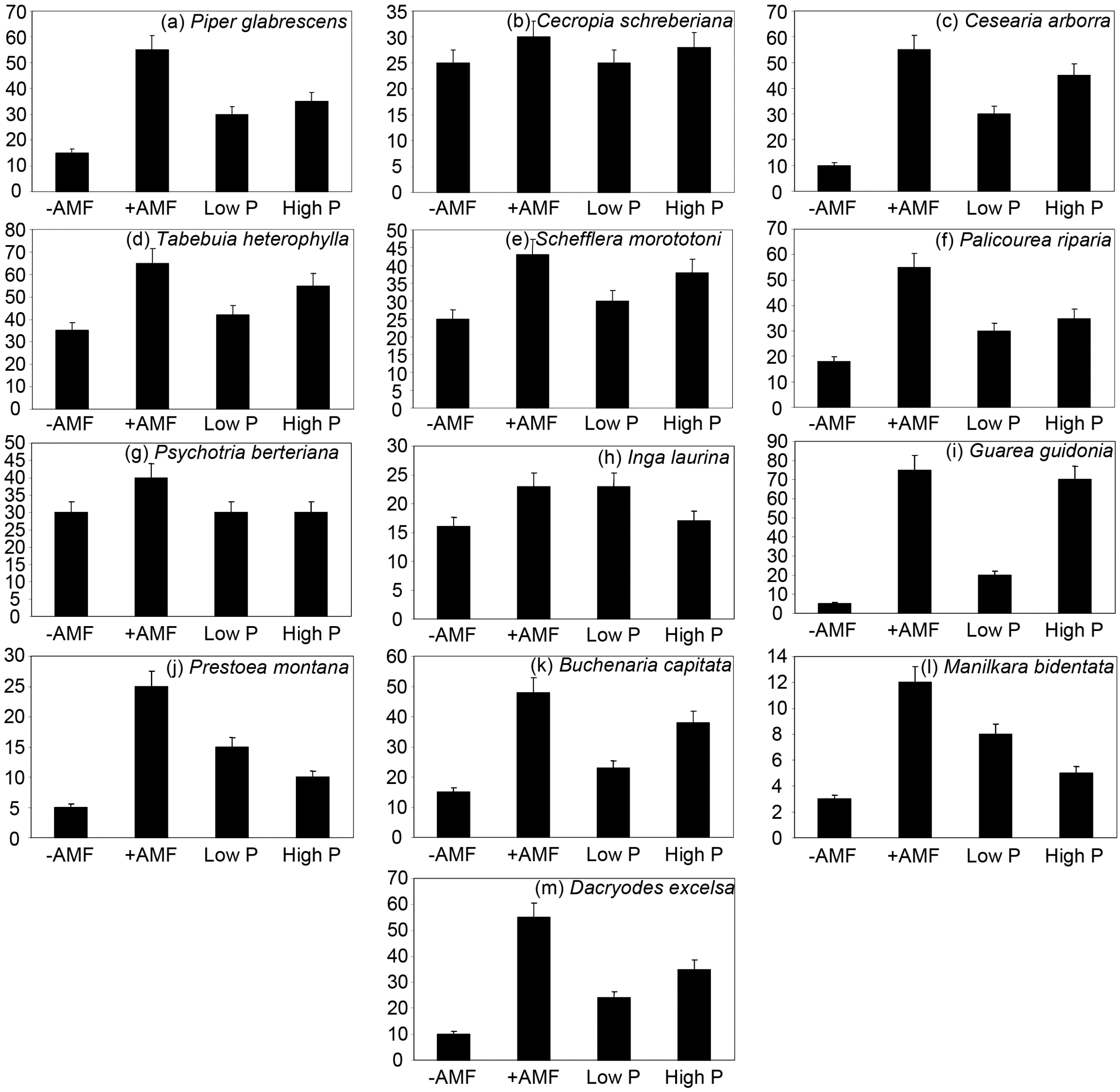

Figure 1 Per cent of roots colonised by arbuscular mycorrhizal fungi (AMF) of (a) *Piper glabrescens*, (b) *Cecropia schreberiana*, (c) *Casearia arborea*, (d) *Tabebuia heterophylla*, (e) *Schefflera morototoni*, (f) *Palicourea riparia*, (g) *Psychotria berteriana*, (h) *Inga laurina*, (i) *Guarea guidonia*, (j) *Prestoea montana*, (k) *Buchenaria capitata*, (l) *Manilkara bidentata* and (m) *Dacryodes excelsa* for the main effects of AMF addition and phosphorus level; means (n = 5) and standard error bars are presented

field. Wood density (Nascimento et al. 2005) and drought tolerance did not do as well as shade tolerance in corresponding with the AMF results. This suggested a secondary role for them but a large role for shade tolerance in defining neotropical tree life-histories (Easdale et. al. 2007).

Several individual species results agreed with past investigations into their mycotrophic strategy: (1) *Inga* sp. were facultatively mycorrhizal because P addition resulted in less AMF colonisation with per cent colonisation between 17 and 31% (Myster 2006), (2) *Cecropia* sp. were either non-mycorrhizal or weakly facultative under certain soil P conditions (DJ Lodge, personal communication) and (3) *Prestoea* sp. were obligately-mycotrophic (DJ Lodge, personal communication). Other

Table 2 The 13 test species sorted in increasing order of AMF dependency

No.	Species	Seed mass[a]	Wood density[b]	Shade tolerance[c]	Drought tolerance[d]
1.	*Cecropia schreberiana*	2	1	1	1
2.	*Schefflera morototoni*	5	na	1	1
3.	*Inga laurina*	8	5	2	2
4.	*Casearia arborea*	3	na	2	2
5.	*Guarea guidonia*	9	2	3	3
6.	*Manilkara bidentata*	12	7	4	4
7.	*Psychotria berteriana*	7	na	5	5
8.	*Prestoea montana*	10	na	5	5
9.	*Tabebuia heterophylla*	4	4	3	3
10.	*Piper glabrescens*	1	na	3	3
11.	*Palicourea riparia*	6	na	na	na
12.	*Buchenaria capitata*	11	6	na	na
13.	*Dacryodes excelsa*	13	3	5	5
	Spearman coefficient	0.90**	0.52	0.70*	0.70*

[a]From Table 1 and http: //www.kew.org/data/sid, [b]Reyes et al. (1992), [c]Devoe (1989), Poorter and Bongers (2006), [d]Condit et al. (1995), Abbott-Wood (2002); * = $0.05 > p > 0.01$, ** = $0.01 > p > 0.001$, na = unavailable data and not used in analysis; numbers under the columns seed mass, woody density, shade tolerance and drought tolerance refer to the original rankings of the test species given to the left of their names

investigations had suggested that *Alchornea latifolia* and *Ochroma pyramidale* were obligate, and *Clibadium erosum* and *Solanum toruum* were strongly facultative (DJ Lodge personal communication).

Tropical tree life histories

Responses of the test species showed the different AMF strategies that neotropical trees and shrubs had for forming an association with AMF. These strategies may be combined with additional plant traits to suggest general neotropical tree life histories (Lugo & Zimmerman 2002). For example, obligate species are thought to have hairless superficial root systems near the surface consisting of coarsely branched, thick roots. In addition, facultatively mycotrophic species may be able to accumulate phosphate in their tissues more than other plants when it is abundant. However, they may not be able to take fungus off existing roots, thereby reducing future infection when P availability is high and leading to time-lag in growth responses. Non-mycotrophic species may also have small seeds with extensive fine/fibrous root systems. These species may be able to take advantage of soil mineral fluxes, making organic acids that aid in making soil phosphate more soluble. Shade tolerance may also be included in strategies because light levels may also affect AMF colonisation with the greatest per cent at higher light levels (Gehring 2003).

Tropical tree life-history studies should be investigated on individual species, not on successional groups (as in Zangaro et. al. 2000) and include traditional traits of seed size, shade/drought tolerance and growth rate, and also traits related to AMF formation and N_{2-} fixation. For example studies have shown successional species responding more to added P and added N than primary canopy species at high light levels (Fetcher et. al. 1996), little or no colonisation response to fertilisation at low light levels (Denslow et. al. 1990), and complex interactive effects of N and P, so important to neotropical rainforest regeneration and dynamics, being most apparent at high light.

Life histories may fall out on main axes of shade tolerance (Easdale et. al. 2007) and tree size (Nascimento et al. 2005) but with important variation among different life stages of each species. Leaf traits such as life span and specific leaf area are good predictors of plant performance and life history (Poorter & Bongers 2006). We concur with Clark and Clark (1992) in a call for measurement of new traits not related to gap dependence and shade tolerance for which trade-offs and correlations have not been found such as root architecture and other aspects that may be related to mycorrhizal dependence. Longer-term data on neotropical tree distribution, abundance, and association (visit http://luq.lternet.edu for details) are also needed along with further complementary experimental studies of their life-history traits.

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REFERENCES

Abbott-Wood C. 2002. Landscape forest modeling of the Luquillo Experimental Forest, Puerto Rico. MSc thesis (Environmental Science), University of North Texas, Denton.

Clark DA & Clark DB. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62: 315–344.

Cluett HC & Boucher DH. 1983. Indirect mutualism in the legume *Rhizobium* mycorrhizal fungus interaction. *Oecologia* 59: 405–408.

Condit R, Hubbell SP & Foster RB. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecology Monograph* 65: 419–439.

Denslow JS, Schultz JC, Vitousek PM & Strain BR. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165–179.

Devoe NN. 1989. Differential seedling and regeneration in openings and beneath closed canopy in sub-tropical wet forest. PhD dissertation, Yale University, New Haven.

Easdale TA, Healey JR, Grau HR & Malizia AA. 2007. Tree life histories in a montane subtropical forest: species differ independently by shade tolerance, turnover rate and substrate preference. *Journal of Ecology* 95: 1234–1249.

Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernandez DS & Lawrence DT. 1996. Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology* 84: 331–341.

Francis JK & Rodriguez JA. 1993. *Seeds of Puerto Rican Trees and Shrubs: Second Installment.* Research Note SO–374. USDA Forest Service, Asheville.

Gehring CA. 2003. Growth responses to arbuscular mycorrhizae by rain forest seedlings vary with light intensity and tree species. *Plant Ecology* 167: 127–139.

Grubb, PJ. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.

Hartnett DC & Wilson GWT. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187–1195.

Janos DP. 2007. Plant responsiveness to mycorrhizas differ from dependence upon mycorrhizas. *Mycorrhiza* 17: 75–91.

Kiers ET, Lovelock CE, Krueger EL & Herre EA. 2000. Differential effects of tropical arbuscular mycorrhizal fungal inocula on root colonization and tree seedling growth: implications for tropical forest diversity. *Ecology Letters* 3: 106–113.

Kottke IA, Beck F, Oberwinkler J, Homeier J & Neill D. 2004. Arbuscular endomycorrhizas are dominant in the organic soil of a neotropical montane cloud forest. *Journal of Tropical Ecology* 20: 25–129.

Li H, Yang G, Shu H,Yang Y, YE B, Nishida I & Zheng C. 2006. Colonization by the arbuscular mycorrhizal fungus *Glomus versiforme* induces a defense response against the root-knot nematode *Meloidogyne incognita* in the grapevine (*Vitis amurensis* Rupr.), which includes transcriptional activation of the class III chitinase gene VCH3. *Plant and Cell Physiology* 47: 154–163.

Lodge DJ. 1987. Nutrient concentrations, percentage moisture and density of field-collected fungal mycelia. *Soil Biology and Biochemistry* 19: 727–733.

Lovelock CE, Andersen K & Morton JB. 2003. Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment. *Oecologia* 135: 268–279.

Lugo AE & Zimmerman JK. 2002. Ecological life histories. Pp 191–213 in Vozzo JA (ed) *Tropical Tree Seed Manual.* Agricultural Handbook 721. USDA Forest Service, Asheville.

Luh-Huang CY & Schultz EE. 1985. Digestion of plant tissue for analysis by ICP emission spectroscopy. *Communications of Soil Science and Plant Analysis* 16: 943–958.

Mabberley, DJ. 1992. *Tropical Rain Forest Ecology.* Chapman & Hall, New York.

Myster RW. 2006. Light and nutrient effects on growth and allocation of *Inga vera* (Leguminosae), a landslide tree in Puerto Rico. *Canadian Journal of Forest Research* 36: 1121–1128.

Myster RW. 2007. *Post-Agricultural Succession in the Neotropics.* Springer-Verlag, Berlin.

Myster RW & Fernandez DS. 1995. Spatial gradients and patch structure on two Puerto Rican landslides. *Biotropica* 27: 49–159.

Nascimento HEM, Laurance WF, Condit R, Laurance SG, D'Angelo S & Andrade AC. 2005. Demographic and life-history correlates for Amazonian trees. *Journal of Vegetation Science* 16: 625–634.

Poorter L & Bongers F. 2006. Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87: 1733–1743.

Reyes G, Brown S, Chapman J & Lugo AE. 1992. *Wood Densities of Tropical Tree Species.* General Technical Report SO:88. USDA Forest Service, New Orleans.

Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.

Whipps JM. 2004. Prospects and limitations for mycorrhiza in biocontrol of root pathogens. *Canadian Journal of Botany* 82: 1198–1227.

Zangaro W, Bononi VLR & Trefen SB. 2000. Mycorrhizal dependency, inoculums potential and habitat preference of native woody species in south Brazil. *Journal of Tropical Ecology* 16: 603–622.

Zangaro W, Nisizaki SMA & Domingos JCB. 2003. Mycorrhizal response and successional status in 80 woody species from south Brazil. *Journal of Tropical Ecology* 19: 603–621.