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Vesicular-arbuscular mycorrhizae of epiphytes

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Abstract. This article introduces reports concerning the occurrence of mycorrhizae on epiphytes in Costa Rica, Ethiopia, Venezuela, Malaysia, and Mexico. Association of vesicular-arbuscular mycorrhizal fungi with the roots of epiphytes is not well known. Vesicular-arbuscular mycorrhizal fungi (VAM) do occur in the canopy, but are uncommon except in certain sites and host taxa. Occurrence of VAM on epiphytes may be constrained by mineral nutrient availability and spatial heterogeneity in the canopy. Nevertheless, epiphytes present unique opportunities to study influences of mycorrhizae on vascular plant community composition and on the evolution of mycorrhizal associations.

Key words: Tropics – Mycotrophy – Spore dispersal – Community composition – Evolution

Introduction

In humid tropical forests, especially those at middle and higher elevations – the mist-shrouded "cloud forests" – trees bear conspicuous, heavy loads of vascular epiphytes on their branches and trunks. Because these can be many meters above the ground, and little is known of vectors of glomalean fungi in wet tropical habitats, the occurrence of vesicular-arbuscular mycorrhizal fungi (VAM) on epiphytes has been an enigma. The articles collected in this issue of *Mycorrhiza* demonstrate that glomalean fungi and VAM do occur in the canopy and on trunks, but are of low frequency and abundance except in certain locales and microsites. Because of the ways in which the canopy differs from the terrestrial environment, further study of epiphyte mycorrhizae has the potential to enhance understanding of the influence of mycorrhizae on epiphyte community composition and on the evolution of mycotrophism.

Mycorrhizae of epiphytes

Autotrophic epiphytes are plants that grow upon other plants which provide physical support but are not directly parasitized (Benzing 1990). Hemiepiphytes, although physically supported by hosts, are at some time rooted in terrestrial soil. Epiphytes that inhabit the canopy or ground interchangeably are called "facultative epiphytes" (Benzing 1990), implying that those restricted to life in the canopy may be called "obligate epiphytes".

In the tropics, many species of Orchidaceae and Ericaceae are epiphytic and, when mycorrhizal, have characteristic types of mycorrhizae (Bermudes and Benzing 1989; Lesica and Antibus 1990), although they have not been surveyed extensively. However, the mycorrhizal status of epiphyte species in other predominant families of vascular epiphytes, such as the Araceae, Bromeliaceae, Cyclanthaceae, Piperaceae, and those of ferns has been an open question. Terrestrial members of several of these families are known to form VAM (used in the generic sense to include both vesicular-arbuscular and arbuscular, gigasporaceous mycorrhizae) including many aroids (Araceae: Janse 1896; Gallaud 1905; Maeda 1954; St. John 1980), pineapple (Bromeliaceae: *Ananas comosus* (L.) Merr.; Lin et al. 1987), Panama hat "palm" (Cyclanthaceae: *Carludovica palmata* R. & P.; Janos 1980a), several members of the black pepper family (Piperaceae: see references in Maffia et al. 1993), and ferns (Maeda 1954; Boullard 1979). Thus, if epiphytic members of families other than the Orchidaceae and Ericaceae have mycorrhizae, they are most likely to have VAM.

Canopy and terrestrial habitat differences

The canopy habitat differs from the terrestrial in several ways that may influence mycorrhiza formation. Mineral nutrient availability and spatial heterogeneity can markedly differ between canopy and terrestrial soil environments.

Availability of soluble mineral nutrients in the canopy is thought to be generally low, although not always (see Lesica and Antibus 1990). Precipitation and atmospheric particulates are the major inputs (Nadkarni and Matelson 1991). Precipitation that flows down stems after interception by leaves can contain leaf leachate with relatively high potassium and calcium concentrations (Benzing 1990), another "input" to the canopy habitat. Organic litter can accumulate in leaf axils, at branch junctions, and along horizontal branch surfaces, especially those proximal to the trunk. When penetrated by interwoven epiphyte roots, the litter and roots comprise canopy organic "mats" (see Maffia et al. 1993). Organic forms of mineral nutrients may be relatively abundant in such mats (Nadkarni 1984), but decomposition and nutrient release can be slow (Nadkarni 1986).

The canopy can become effectively xeric, especially at its periphery, when it is not raining (see Benzing 1990). Consequently, most epiphytes have adaptations for water conservation or storage, and cacti even occur as epiphytes in the wet Neotropics. The crassulacean acid metabolism (CAM) photosynthetic pathway is prevalent among some groups of epiphytes such as bromeliads, and variants of CAM occur in the genus *Peperomia.* Although fluctuating moisture availability in mesic canopies, together with generally low availability of soluble mineral nutrients might confer advantages to epiphytes with VAM, the ability of CAM plants to sustain the energetic cost of mycorrhizae should be investigated.

In addition to periodic moisture and putative nutrient stresses, the canopy environment has extreme spatial and temporal heterogeneity. In contrast to the thin, superficial root zone of a tropical soil (see Janos 1984), the canopy is laterally discontinuous, and has a pronounced vertical dimension that may result in light, temperature, and humidity gradients. Epiphyte species may specialize on certain positions in the canopy, and VAM species with different temperature (see Janos 1987) or dessication tolerances might similarly specialize. Temporally, branch and tree falls completely eliminate canopy habitat, thereby making the succession of epiphytes on eventual replacement trees a "primary" succession requiring new introduction of mycorrhizal propagules (see Janos 1980b; Maffia et al. 1993).

So little is known about the dispersal of VAM in tropical forests that the way in which they may reach the canopy is open to speculation (e.g., Michelsen 1993). Several species of Glomales have been reported from cloud forest canopy organic mats in Costa Rica (Vargas 1990). Glomalean spores usually are not abundant in wet tropical soils (Janos 1992), so soil movement is not likely to account for much dispersal to the canopy. Birds that contact soil or utilize VAM-bearing material for nests (McIlveen and Cole 1976) might carry some propagules to the canopy, as might arboreal-nesting, ground-foraging arthropods such as ants. Terrestrial harvester ant mounds in the northern temperate zone (Friese and Allen 1988) and nests of the genera *Erebomyrma* (= *Spelaeomyrmex*), *Pheidole*, and *Solenopsis* (*Diplorhopterum*) in the tropics (C. R. Carroll, University of Georgia, personal communication; Janos, personal observation) can contain many spores. In the tropics, however, it is not known if sporulation in situ is stimulated by root pruning activity of the ants or if the ants gather lipid-rich spores. If the latter, then similar behavior by arboreal nesting ants might disperse spores to the canopy. The most significant dispersal agent of VAM propagules to the canopy, however, may be scansorial rodents. Bakarr et al. (1990) found glomalean spores in the feces of the scansorial *Peromyscus nudipes* in a Costa Rican cloud forest.

Discussion

The very limited literature available on the mycorrhizal status of epiphytes, together with the articles in this issue, may provide more questions than answers concerning epiphyte mycorrhizae. I contend that the canopy is an extreme habitat for VAM fungi, and as such, offers special opportunities to advance understanding of mycorrhiza ecology and evolution.

Community dynamics

VAM are generally considered ubiquitous in terrestrial soils, although I have argued (Janos 1980b, 1992) and others have found (see Allen 1991), that some terrestrial habitats can lack VAM. Many habitats likely comprise small-scale mosaics of significantly different potentials to form mycorrhizae. Although small-scale heterogeneity in VAM formation can be difficult to demonstrate in terrestrial soils by conventional methods, such heterogeneity in the canopy is indisputable. At the scale of the anastomosing structure of branch crowns, mycorrhizal fungi can spread only linearly along branches from points of inoculum introduction. Moreover, bare branches with smooth bark may periodically become too dry for hyphae to survive. Notwithstanding, Maffia et al. (1993) and Rabatin et al. (1993) comment on the abundance of coarse VAM hyphae external to roots in the canopy, especially where organic matter has accumulated. Their observations raise the complementary questions of which epiphyte species provide photosynthate to sustain these hyphae, and whether or not the fungi have some ability to live non-mutualistically (see Hepper and Warner 1983).

Tree falls and the succession of new trees which replace them make natural forests mosaics of different-aged tree crowns. Consequently, forest canopies comprise a melange of epiphyte community seral stages superimposed on whatever within-crown niche partitioning by position may exist among epiphyte species. However, examination of epiphytes in even-aged tree stands of known age such as cacao, oil palm (but see Nadarajah and Nawawi 1993), rubber or timber tree plantations might elucidate mycorrhiza effects on succession. Questions needing answers include: how frequently are VAM dispersed to the canopy, what are their vectors and the relative importance of these vectors, and, once established at a point in the canopy, how quickly do VAM spread, both as growing hyphae and by downward flow of propagules (see Maffia et al. 1993)?

Although Vargas (1990) did not find an appreciable difference between canopy and terrestrial VAM community composition in a Costa Rican cloud forest, Rabatin et al. (1993) found pronounced differences in Venezuelan cloud forests. Gradients of light, temperature, and humidity within single tree crowns, the entire canopy, or from site to site (see Michelsen 1993; Rabatin et al. 1993) might facilitate testing the potential of species of Gigasporineae to tolerate more xeric conditions than species of Glomineae. The latter are more common than the former in tropical wet forest terrestrial soils (see Sieverding 1991).

Evolution

As a frontier for mycorrhiza research, the canopy may offer insights concerning the evolution of dependence of plant species on VAM and the evolution of the mycorrhiza mutualism itself.

Although the terms “obligately mycotrophic” and “facultatively mycotrophic” (see Stahl 1900, cited in Allen 1991; Janos 1980a, b) are used by mycorrhiza researchers to describe the requirement for mycorrhizae by a plant species, what authors precisely mean by these terms may differ. In general, “facultatively mycotrophic” means “capable of growing without mycorrhizae in fertile substrates, although forming and benefiting from mycorrhizae in infertile media”. I suggest that there are two important corollaries to this definition.

The first corollary is that “facultatively mycotrophic” describes the *dependence* of a plant species on mycorrhizae for survival and growth, i.e., whether or not individuals of the species can grow without mycorrhizae at a particular fertility, not how much they grow when mycorrhizal (Janos 1988; see also Sieverding 1991). Thus, the term refers to an intrinsic property of a vascular plant species which is presumably genetically based. The term *responsiveness* (to mycorrhizae) can be used to indicate how well a plant grows when experiencing a particular mycorrhizal fungus (or fungi) and soil in combination. Responsiveness is a conjoint attribute of a plant species, mycorrhizal fungus, and soil. Plant dependence and responsiveness do not necessarily covary. For example, a plant that cannot grow without mycorrhizae even at the highest fertility it encounters in natural habitats (i.e., an obligate mycotroph) may not grow rapidly even with mycorrhizae. It is true, however, that an extremely facultatively mycotrophic plant species is not likely to be very responsive to mycorrhizae under any conditions.

The second corollary to the definition of facultative mycotrophy is that what constitutes a “fertile substrate” to a facultatively mycotrophic species need not be very fertile on an absolute scale. Epiphytes able to survive, grow and reproduce without mycorrhizae, notwithstanding putative low nutrient availability in the canopy, exemplify this. Because the canopy environment may require epiphyte species to be “stress tolerators” more than “competitors” (see Grime 1977), slow growth rates in the canopy need not disadvantage a species. Ironically, although mycorrhizae are typically considered an adaptation to nutrient stress, widespread lack of VAM inocula throughout the canopy and the energy cost of mycorrhizae may be “stresses” to which epiphytes must adapt.

Whether or not obligate mycotrophy is a plesiomorphic character state of vascular plants (Nicolson 1975; Pirozynski and Malloch 1975; Trappe 1987), terrestrial tropical soils are typically depauperate in available phosphorus, and obligate mycotrophy is common (Janos 1987). If epiphytes evolved from terrestrial progenitors, this is likely to have involved a transition from obligate to facultative mycotrophy. In general, any of three natural selection pressures might favor the evolution of reduced dependence upon mycorrhizae: 1) regular failure to encounter mycorrhiza inocula such that only those individuals capable of some growth without mycorrhizae survive, 2) frequent encounter of high fertility such that an individual that avoids the energy cost of mycorrhizae, which are not needed, achieves the greatest reproductive success, or 3) inability to sustain the energy cost of mycorrhizae such that individuals able to reject mycorrhizae, notwithstanding low soil fertility, perform best. Terrestrial plants that occur in tropical forest understory at very low light levels might exemplify the latter. Maffia et al. (1993) imply that such rejection of mycorrhizae by species of the family Piperaceae preadapted them for epiphytism. These sorts of hypotheses might be tested by comparing the degrees of dependence on mycorrhizae among obligately epiphytic species, facultative epiphytes, and strictly terrestrial congeners. That Nadarajah and Nawawi (1993) did not produce VAM on obligate epiphytes with inocula that did form VAM on facultative epiphytes suggests that among the pteridophytes that they tested, those that are obligately epiphytic may be the most facultatively mycotrophic.

Study of fungi associated with epiphyte roots might be informative with respect to evolution of the mycorrhiza mutualism. Many fungi other than mycorrhizal fungi can be found on epiphyte roots, and sometimes within them (see Bermudes and Benzing 1989). In a survey of approximately 1826 cm of epiphyte fine roots sampled haphazardly in Ecuador by David Benzing from a variety of epiphyte species, Todd Skeen and David Janos (unpublished data) found mycorrhizae in only nine of 59 samples (15%). Twenty of the samples that lacked mycorrhizae (20/50 = 40%), however, included apparently saprophytic or parasitic fungi. This underscores a need for caution in deciding what is a mycorrhizal fungus when studying epiphyte mycorrhizae. Holocarpic, endobiotic chytrid sporangia within roots can stain dark blue with trypan blue in lactoglycerol, and under the dissecting microscope may be mistaken for VAM vesicles.

The scarcity of soluble mineral nutrients in the canopy and the accumulation of organic forms probably confers an advantage upon plants associated with fungi that produce cellulase or lignases and can thereby directly access organic mineral nutrients. Does the "fine endophyte", *Glomus tenue* (Greenall) Hall, which Rabatin et al. (1993) commonly found associated with epiphytic bromeliads in Venezuela owe its extensive colonization of the canopy in part to such ability? Can the brown, septate fungus that Allen et al. (1993) found consistently associated with bromeliad roots in Mexico directly access mineral nutrients in organic matter? The lack of an apparent host defensive reaction noted by Allen et al. (1993) suggests that the association might be mutualistic. If so, then we must expand our definition of a mycorrhiza accordingly.

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