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Research article

Have male trees of the tropical rain forest evolved to minimize the interactions with mycorrhizal symbionts?

Rocío Vega-Frutis[a,b], Juan Carlos López[c], Citlalli Flandes[a], Roger Guevara[a,*]

[a] Red de Biología Evolutiva, Instituto de Ecología, A.C., Carretera Antigua a Coatepec 351, El Haya, C.P 91070 Xalapa, Veracruz, Mexico
[b] Programa de Biología, Unidad Académica de Agricultura, Universidad Autónoma de Nayarit, Km. 9 Carretera Tepic-Compostela, C.P 63780 Xalisco, Nayarit, Mexico
[c] Centro de Investigaciones Tropicales (CITRO), Universidad Veracruzana, Ex-Hacienda Lucas Martín, Privada Araucarias, C.P 91110 Xalapa, Veracruz, Mexico

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ABSTRACT

While arbuscular mycorrhizal fungi improve plant performance they demand large shares of the plant's assimilated carbon, therefore resource allocation trade-offs may drive the commonly observed sexual dimorphism in mycorrhizal colonization in dioecious species. Here we looked for evidence of the evolutionary reduction of mycorrhizal colonization in males of 15 tropical rain forest plants including palms (*Chamaedorea*) and trees, light-demanding and shade-tolerant species. For none of the analyzed species there was evidence of spatial segregation of the sexes. Most of the tree species had no seasonal variability in mycorrhizal colonization and males had lower mycorrhizal colonization than females in over 70% of the tree species. In contrast, there were no differences between the sexes of the *Chamaedorea* species. *Chamaedorea* species had ticker roots and lower specific root length than trees, and seasonal patterns of mycorrhizal colonization correlated with the life-histories of the plants. Based on phylogenetically independent contrast, mycorrhizal colonization of male trees correlated negatively with a metric of sexual differentiation of mycorrhizal colonization between sexes. Our results suggest an evolutionary reduction in the intensity of mycorrhizal interactions in male plants, presumably driven by resource allocation trade-offs as the origen of sexual dimorphs in mycorrhizal colonization.

1. Introduction

Dioecy (separate female and male plants) has evolved in up to 38–43% of the plant families, including 6% of the angiosperm species worldwide (Renner and Ricklefs, 1995; Barrett, 2002). However, in tropical regions, dioecy occurs in up to 21% of the flowering plant species (Bawa, 1980). Many dioecious species display secondary sexual dimorphism; that is, differences between male and female plants in traits not involved directly in the production of gametes (cf. Geber et al., 1999). Secondary sexual dimorphism between male and female plants includes morphological traits, for instance, the size and number of flowers produced in male and female plants (e.g., Delph, 1999; Hemborg and Karlsson, 1999), and differences in physiological traits such as photosynthesis rates, the uptake of nutrients, and the production of secondary metabolites (e.g., Crawford and Balfour, 1983; Ågren, 1988; Dawson and Bliss, 1989; Leigh and Nicotra, 2003; Wheelwright and Logan, 2004; Cornelissen and Stiling, 2005; Hultine et al., 2008). Male and female plants may also have different life history traits such as the time to flowering (e.g., Thomas and LaFrankie, 1993; Delph, 1999; Saeki, 2008), or different functional traits such as anti-herbivore and anti-parasite defense mechanisms. Male and female plants may also offer rewards of different quality or quantity for mutualistic species such as pollinators and mycorrhizal fungi (e.g., Cepeda-Cornejo and Dirzo, 2010; Vega-Frutis et al., 2013a). Secondary sexual dimorphism has commonly been linked to the resource allocation trade-offs imposed by the difference in the reproductive costs of male and female plants, with females investing proportionally more resources in reproduction than males as a general rule (Reznick, 1985; Delph, 1999; Obeso, 2002), although some exceptions have been documented in which males have a more costly reproduction than females (Delph et al., 2005). Secondary sexual dimorphism stems from a set of differentiated processes and mechanisms that maximize gains (e.g., nutrient acquisition and pollination) and minimize costs in male and female individuals; these can have substantial ecological and evolutionary

* Corresponding author.
E-mail address: roger.guevara@inecol.mx (R. Guevara).

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consequences and can alter, for instance, antagonistic and mutualistic interactions in male and female plants (Cepeda-Cornejo and Dirzo, 2010).

No less than 74% of flowering plants, distributed in almost all terrestrial biomes, are associated with arbuscular mycorrhizal (AM) fungi (Brundrett, 2009). Hyphae of mycorrhizal fungi proliferate in the root cortex and grow into the soil matrix where they facilitate the uptake of water and soil nutrients (especially phosphorus and nitrogen) by their host plants (Koide, 1991; Lee and George, 2005; García et al., 2008). However, AM fungi are expensive symbionts and they can consume 4–30% of the photosynthates produced by their host plants (Jakobsen and Rosendahl, 1990; Finlay and Söderström, 1992). Therefore, the resource allocation theory predicts that plants will allocate resources to mycorrhizal fungi when plant growth and reproduction are limited by soil nutrients (Treseder, 2004), providing that carbon assimilation is not, and does not become, a limiting factor for plant growth and reproduction (Aguilar-Chama and Guevara, 2012).

Differences in mycorrhizal colonization between male and female plants of dioecious species in response to changes in soil fertility suggest that the reduction of mycorrhizal colonization in fertile soils may be more than just an ecological response of the host plants. A study with the pioneer tropical tree *Carica papaya* showed that female trees have a higher investment in mycorrhizal symbionts than male plants, and mycorrhizal colonization in female plants correlated negatively with the availability of phosphorus in the soil, whereas mycorrhizal colonization of male plants did not change with soil fertility (Vega-Frutis and Guevara, 2009). *C. papaya* grows in dense patches in forest gaps and roadsides, and the roots of male and female plants are often knitted together in the soil. Therefore, the different responses of male and female plants to changes in soil nutrient availability (Vega-Frutis and Guevara, 2009) may have nothing to do with spatial segregation of the sexes but rather with the evolution of different strategies in male and female trees to deal with mycorrhizal interactions (Vega-Frutis and Guevara, 2009). Eppley et al. (2009) suggested that mycorrhizal interactions may be involved in the spatial segregation of the sexes of *Distichlis spicata*. However, spatial segregation of sexes seems an unlikely explanation for secondary sexual dimorphism in mycorrhizal colonization. The general rule in species with spatial segregation of sexes is that female plants proliferate in less stressful sites, for instance, sites with high soil fertility or water availability, compared with those sites in which males are more frequent or abundant (Bierzychudek and Eckhart, 1988). Thus, because low soil fertility environments favor mycorrhizal colonization (Treseder, 2004), males should have higher mycorrhizal colonization than female plants, and this would appear to contradict the commonly observed patterns in which female plants have a greater mycorrhizal colonization than male plants, for example, in the dioecious perennial herbs *D. spicata* (Eppley et al., 2009) and *Antennaria dioica* (Varga and Kytöviita, 2010a; Vega-Frutis et al., 2013b), or gain more benefits from mycorrhizal colonization as in the perennials *A. dioica* (Varga and Kytöviita, 2008) and the gynodioecious species (female and hermaphrodite individuals) *Geranium sylvaticum* (Varga and Kytöviita, 2010b). In *A. dioica*, females gain more phosphorus than male plants when associated to mycorrhizal fungi, and in *G. sylvaticum*, mycorrhizal fungi are critical to explain the larger size of the female plants compared with those of the hermaphrodites. However, other studies with *A. dioica* (Varga and Kytöviita, 2008, 2011, 2012) showed no differences in mycorrhizal colonization between the sexes (but see Vega-Frutis et al., 2013c).

Dioecy is believed to have evolved independently in many plant lineages from hermaphroditic ancestors either through gynodioecy or monoecy (Charlesworth and Charlesworth, 1978; Ainsworth, 2000; Barrett, 2002) as a mechanism that maximizes allogamous breeding. If mycorrhizal interactions had no primary role in the evolutionary separation of sexes in different individuals, then newly evolved unisexual plants would be expected to have had expressed mycorrhizal colonization patterns similar to those in their hermaphroditic ancestors. Thus, we hypothesize that the low mycorrhizal colonization reported in male plants compared with female plants of dioecious species may be the result of evolutionary reductions in the intensity of mycorrhizal interactions in male plants, whereas female plants kept the levels of colonization of their hermaphroditic ancestors. Given that dioecy is widespread across phylogenetic clades of plants, we included in our analysis monocotyledons and dicotyledons, and also light-demanding and shade-tolerant species (Swaine and Whitmore, 1988), and we sampled in three different seasons to include seasonal variability.

Plant life history and seasonality are known to affect mycorrhizal colonization. For instance, Zangaro et al. (2003) found a clear reduction of mycorrhizal colonization from pioneer to early secondary to late secondary and to climax species in the Tibagi River Basin, Paraná State, in south Brazil. Also, Zangaro et al. (2007) found that the mycorrhizal responsiveness of plants was higher in early successional than in late successional species, and mycorrhizal colonization altered root morphology in early successional species but had no effect on late successional species.

Mycorrhizal colonization is also usually higher during the plant growing season, which is a pattern that includes species with inverted phenology (Diop et al., 1994; Allen et al., 1998). In addition to sexual dimorphism in mycorrhizal colonization, we predict higher mycorrhizal colonization in light-demanding species than in shade-tolerant species, and also higher colonization of the roots by mycorrhizal fungi during the summer and winter rainy seasons than in the dry season. We aim to answer the following questions. Is there sexual dimorphism in mycorrhizal colonization in tropical plant species with different life histories and phylogenetic relatedness? Do female plants have higher mycorrhizal colonization than male plants? Are there differences in mycorrhizal colonization between plants with different life histories? Are seasonal changes in mycorrhizal colonization equal in plants with different life histories? Given that light-demanding and shade-tolerant species usually differ in the frequency of AM colonization, we predicted higher AM colonization in the roots of light-demanding species. Also we predicted higher AM colonization in female plants of both life history strategies, irrespective of their phylogenetic relationship because the costs to reproduction are assumed to be high in female plants of either life history strategy. However, if the sexes were spatially segregated, our predictions could potentially be explained by differences in microenvironmental conditions rather than by the sex allocation theory. Therefore, we investigated sex spatial distribution of the plant species studied. Finally, to help us explain the observed patterns we considered the root morphology of the studied species. Recent studies have shown that root morphology traits are important determinants of mycorrhizal colonization (Kong et al., 2014) and these traits (e.g., first-order root diameter and specific root length) are known to be phylogenetically conserved and have limited plasticity compared to root architectural traits (e.g., root branching ratio) which vary widely with environmental conditions (Chen et al., 2013; Liu et al., 2015).

2. Materials and methods

2.1. Study site

The study was conducted at the Tropical Biology Station Los Tuxtlas (Universidad Nacional Autónoma de México) in southern Veracruz, Mexico (18°34′–18°36′ N, 94°04′–95°09′ W). The 600 ha protected area ranges in elevation between 150 and 530 m, and the climate is warm and humid for most of the year. The annual