



Root parasitism by *Scybalium fungiforme* Schott & Endl. is not random among host species in seasonal tropical forest

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ABSTRACT

Though they comprise 1 % of plant species on the planet, plant parasites are poorly known. They have been considered a threat to cultivated plants and to the conservation of host species in natural areas. Due to the complex interactions they have with their hosts, understanding their biology is fundamental to the development of conservation strategies for both parasite species and their hosts. We sampled two populations of the root parasite *Scybalium fungiforme* (Balanophoraceae) in seasonal tropical forest fragments to identify its host species and their functional attributes. Among the hosts, *Croton floribundus* seems to be preferred (68 % of parasitized plants), while four liana species were complementary hosts (32 %). Host species preference differed sharply among fragments and seems to be related to the successional stage of these forests. The hosts *C. floribundus* and the four liana species are perennial, fast growing and have large vessels, all of which are attributes that enable high water and nutrient acquisition efficiency. Despite a lack of clear host specificity at the species level, functional convergence among parasitized species suggests that host specificity is mediated by functional traits.

Keywords: Balanophoraceae, *Croton floribundus*, holoparasitism, host specificity, lianas

Introduction

Most parasitic plant species are angiosperms, among which parasitism has evolved independently. Plants from this functional group (Těšitel 2016) have been reported as regulators in plant communities, having a key role in the maintenance of biodiversity (Windsor 1995; Durden & Keirans 1996). These plants occur in natural and managed ecosystems and comprise more than 4500 species and 268 genera, belonging to 22 botanical families and representing

about 1 % of the world plant species (Press & Phoenix 2005; Nickrent 2008). Although the influence of parasite plant species on the performance of its hosts is well documented (*i.e.* Kim *et al.* 2019; Lopez *et al.* 2019; Mursidawati *et al.* 2019), other biological and ecological aspects of these species still remain unexplored (Bardgett *et al.* 2006). In general, most parasitic plant species are pollinated by insects and some vertebrates, and their main seed dispersers are birds and mammals (Bellot & Renner 2013; Lehn *et al.* 2015; Freitas *et al.* 2017). The strategic mechanisms of resource acquisition and absorption by parasitic plants are still poorly

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understood (Freitas *et al.* 2017). This gap might be explained, in part, by the fact that these plants partially (hemiparasite) or completely (holoparasite) depend on their hosts to obtain water and nutrients (Gibot-Leclerc *et al.* 2013; Santos *et al.* 2017). Some studies have suggested that parasitic plants can find their hosts through chemical signals in soil, and that they use a special structure, the haustorium, to access the host xylem to obtain resources (Watson 2009).

There is a wide variety in host specificity among parasitic plants at species or genus level (Kuijt 1969; Norton & Lange 1999; Su *et al.* 2012; Guerra *et al.* 2018), and this diversity is essential to understanding historical and ecological aspects that determine the associations between parasite and host (Stireman & Singer 2003). Some studies suggest the existence of functional patterns of parasitism (Ward 1992; Arruda *et al.* 2006) and evolutionary adaptations that increase the reliance of the parasite on the host (Schneeweiss 2007; Conn *et al.* 2015; Těšitel 2016).

Identification of hosts is especially important to parasitic plant conservation, but, in general, studies indicate host lists without differentiating casual hosts from preferential hosts, which are essential to parasite species' survival (Marvier & Smith 1997). In a conservation context, parasitic plants have been especially studied by the threat that they pose to host species (McCallum & Dobson 1995). However, there are studies that defend parasite species conservation (Windsor 1995) and consider them as keystone species, due to the wide variety of effects that they can exert on ecosystems (Press & Phoenix 2005). In general, it is reasonable to conclude that due to their interaction with insects, birds and mammals in pollination and seed dispersal processes (Bellot & Renner 2013; Lehn *et al.* 2015; Freitas *et al.* 2017), parasitic plants can be considered fundamental elements of wide interaction webs.

The Balanophoraceae family, of which *Scybalium fungiforme* is part, is composed of root parasite plants, comprising 18 genus and 50 species occurring around the world (Hansen 1980; Santos *et al.* 2017). In Brazil, seven species of this family have been described (Cardoso 2014), including parasites of different taxonomic and functional groups of hosts, including shrubs, herbs and especially trees (Hansen 1972; 1980; Souza & Lorenzi 2008). Detailed information about Balanophoraceae species are limited, as their aboveground reproductive structures last for short periods of time (Hansen 1972; Hansen 1980; Souza & Lorenzi 2008; Sato & Gonzalez 2016). Flowering and fruiting in the Balanophoraceae are seasonal, occurring in dry periods, potentially serving as alternative food sources for fauna in periods of scarcity (Freitas *et al.* 2017). After a systematic review carried out through the database Web of Science, considering the period from 1987 to 2018, we found 89 publications, including both review and research articles, which investigated different aspects of plant biology within the Balanophoraceae family in its range of occurrence. Ecological interactions and the reproductive systems within

this family have been rarely studied (Freitas *et al.* 2017), despite being fundamental issues to drive biodiversity conservation strategies.

None of the studies analyzed have investigated the species *Scybalium fungiforme*, so this species is practically unknown by science, except by its botanical nomenclature and its occurrence records in botanic collections and in some floristic inventories from remaining seasonal tropical forest fragments (Kinoshita *et al.* 2006; Lombardi *et al.* 2012; Correa *et al.* 2018). Here we aimed to identify the host plants parasitized by *Scybalium fungiforme* in two remnants of seasonal tropical forest in order to assess the occurrence of host specificity for this species.

Materials and methods

Scybalium fungiforme

Scybalium fungiforme Schott & Endl. (Balanophoraceae), known popularly in Brazil as “cogumelo-de-caboclo”, is an herbaceous plant and root holoparasite, whose Latin denomination reflects the morphology of its inflorescence, which resembles a pink to vinaceous fungus emerging from the ground. *Scybalium fungiforme* is monoecious and has unisexual inflorescences (Fig. 1A, B), 8 cm in diameter, with bracts at the base of each branch (Cardoso 2014). Flowers are unisexual, present a perianth, are trimerous with tepals partially fused, tubular at the base and with an irregular shape at the apex (Cardoso 2014). Male flowers are buried in a layer of trichomes, growing about 6 mm, with a tubular part and a tripartite perianth (Hansen 1980; Cardoso 2014). Female flowers present a perianth adnate to the ovary, elliptical and slightly compressed (Hansen 1980; Cardoso 2014). Fruits are oval to oblong, red or brown color, smooth or grooved, with a red or brown color and juicy consistency and containing a single seed (Cardoso 2014). This species also has a high water content, about 80 % of its fresh weight (RA Munis unpubl. res.).

The 65 records of the species' occurrence verified at Species Link online database (<http://www.splink.org.br/>, accessed in 4 Jan. 2019) are concentrated in São Paulo state (44), followed by Minas Gerais (13), with a single record in each of the states Rio de Janeiro, Espírito Santo, Paraná and Distrito Federal, being rarely found in coastal regions. All records including information about the habitat mention forest environments, the majority in seasonal tropical forest, but there are also records in mixed subtropical evergreen forest and gallery forest. From all records, 80 % correspond to material collected during the dry season (winter months, June, July and August), in seasonal tropical forest regions. Apparently, this species does not grow aboveground shoots during warm and rainy seasons, with rare records corresponding to summer and spring months (5 %). Kinoshita *et al.* (2006) reported that the pollination syndrome of the species is myophillia (fly-pollinated).





Figure 1. **A.** Individual of *Scybalium fungiforme* with inflorescences: one pistillate and another in early stage (Bar: 1.59 cm); **B.** Individual of *Scybalium fungiforme* with one staminated (*) inflorescence and two pistillate (+) (Bar: 1.78 cm). **C.** Root of *Croton floribundus* indicated by an arrow, connected to the haustorium and the multilobated tuber (x) of *Scybalium fungiforme* (Bar: 2.72 cm). (Photos taken in a seasonal tropical forest fragment, Botucatu, São Paulo state, Brazil).

Study sites

This study was conducted in two forest fragments (hereinafter Fragment 1 and Fragment 2) at Experimental Farm Edgardia (746 ha), located in Botucatu municipality, São Paulo state, Brazil. The vegetation of these fragments is classified as seasonal tropical forest, a forest type in which 50-70 % of canopy species shed their leaves during the dry season. Previous studies on these forest fragments have recorded high tree species richness, with 61 species being reported by Fonseca & Rodrigues (2000) and 75 species by Jorge & Pereira (2015). The climate in this region is Cfa (Köppen classification, Alvares *et al.* 2013), characterized by

a rainy and warm season from September to April and a dry and cool season from May to August (rainfall below 50 mm), average annual rainfall being about of 1302 mm (Sentelhas *et al.* 2003). The annual average temperature recorded in Botucatu is 20.2 °C, July being the coldest month (average 16.5 °C) and February the hottest (average 23.1 °C) (Sentelhas *et al.* 2003).

Fragment 1, with 110 ha (22°49'19.95"S 48°23'31.70"W, at elevation of 505 m), has suffered disturbances in the past, especially selective exploitation of economically important tree species, with the last harvest occurring between 1975 and 1980 (Jorge & Pereira 2015). Fragment 2 comprises 303 ha (22°48'45.38"S 48°24'54.03"W, at elevation of 556 m), presenting a better conservation status than Fragment 1.

Field data collection: parasite and hosts

We searched for *Scybalium fungiforme* within the two forest fragments where the target species was recorded, totaling 32 hours sampling, from July 23 to July 26, 2018. We sampled 69 individuals of *Scybalium fungiforme*, being 53 in Fragment 1 and 16 in Fragment 2. We carefully dug around each parasitic plant with a garden shovel until finding the main root that was being parasitized. We then unburied the root until finding the host plant, trying not to damage the individuals. We identified the host plants during the field surveys, and when it was not possible, we collected botanical samples for later identification, consulting the literature (Rezende 1997; Udulutsch 2004) and specialists. When finding the host with precision was not possible, we collected root samples to identify the species based on wood anatomy, by comparison with the roots of the other host species, consulting specialized literature descriptions or with specialist's assistance.

After identifying the main hosts of *S. fungiforme*, we used previous floristic surveys of the studied fragments (Cassola 2008; Jorge & Pereira 2015) to evaluate the relative abundance of hosts among families observed in each population of the parasite species.

Results

Based on a total of 69 parasite individuals recorded, we observed only five host species (one tree and four lianas), belonging to three botanical families, predominately Euphorbiaceae by relative abundance, which comprised 68 % of the observations (47 individuals), followed by Malpighiaceae, comprising 22 % (15 individuals) and Bignoniaceae with 9 % (six individuals). The only tree species recorded among the host plants was *Croton floribundus* - Euphorbiaceae (Fig. 1C), while the liana species were *Banisteriopsis adenopoda* - Malpighiaceae, *Fridericia samydoides* - Bignoniaceae, *Bignonia campanulata* - Bignoniaceae and one unidentified liana.

In Fragment 1, 53 individuals of *Scybalium fungiforme* were recorded, of which 45 were parasitizing the species *C. floribundus* (85 %), followed by *F. samydoides* with five parasites (9 %), *B. adenopoda* with two parasites (4 %) and one parasite in *B. campanulata* (2 %). In Fragment 2, 16 individuals were recorded, of which 13 (81 %) were parasitizing *B. adenopoda*, two (13 %) parasitized *C. floribundus* and one parasite was associated with an unidentified species of liana. Pooling our records across fragments, 68 % of *S. fungiforme* occurrences were associated with *C. floribundus*, and 32 % with four species of lianas.

Discussion

The populations of *Scybalium fungiforme* which we sampled are large for a species of relatively rare occurrence,

with only 65 collection records in Brazil (Species Link, <http://www.splink.org.br/>, access in 01/01/2019). The identified host species of *Scybalium fungiforme* were *Croton floribundus*, *Banisteriopsis adenopoda*, *Fridericia samydoides* and *Bignonia campanulata*. The only tree species parasitized was *C. floribundus*, popularly known as “capixingui”. This species is a typical pioneer, short-lived, evergreen, very common in edges and gaps of seasonal and riparian forests in Paraguay and Brazil (Caruzo & Cordeiro 2007). As a fast-growing tree, it can shade out other species, being efficient in exploiting environmental resources (water and nutrients) (Padovan et al. 2018). *Banisteriopsis adenopoda*, *Fridericia samydoides* and *Bignonia campanulata* are lianas (Weiser 2007) widely occurring in seasonal tropical forest and in closed cerrado (cerradão) (Vargas et al. 2018). Though parasitic plants are considered a threat to the conservation of host species populations (McCallum & Dobson 1995), during our field observations we did not find any evidence that parasitized individuals were being impaired by parasitism.

With a large number of *S. fungiforme* individuals sampled and a considerable effort in identifying host plants, we present robust data that indicates a preferential host – the tree species *C. floribundus* – and four liana species that can be considered complementary hosts, since, together, these lianas corresponded to only 32 % of parasitized individuals. Supposing no preference at species level, we would expect a much higher host plant diversity among the hosts, considering that in these forests more than 60 tree species have been recorded (Fonseca & Rodrigues 2000; Jorge & Pereira 2015), along with a probably similar number of liana species, which are normally abundant in seasonal tropical forest fragments (Udulutsch et al. 2004). Our observations complement the study conducted by Cardoso (2014), which suggested that *S. fungiforme* does not present a specific host. In our study, however, despite a not clear specificity at species level, the functional convergence among the hosts suggests a functional preference.

Despite a lack of clear specificity at species level, we found a consistent convergence indicating a functional specificity among the host species. Though lianas are considerably distinct from *C. floribundus* in habit, there are several functional attributes that are common to all species recorded as hosts of *S. fungiforme*. Similar to *C. floribundus*, lianas usually are fast-growing species and efficient in exploiting resources like water and nutrients. Because the narrow stems and the large leaf area, lianas have evolved internal stem structures that provide efficient and fast water transport (Engel et al. 1998; Sande et al. 2019). Some liana species present increased diameter and medium transverse area of conductive vessels and gain efficiency in transport by a lack of transversal walls and by modifications to perforation plates (Peñalosa 1985; Dias et al. 2019). The xylem of lianas can also remain conductive for longer time, compared to trees (Schnitzer et al. 2014). These functional attributes of plants that host *S. fungiforme*



support maximum transference of water and nutrients to parasites, in line with past observations of parasite preferences for hosts with high transpiration rates (Kuijt 1969).

Classical studies about parasitism in plants indicate that parasitic species rarely infect just one host species (Kuijt 1969; Norton & Lange 1999). Despite other studies indicating that the existence of a preferential host is common, other species are often complementarily parasitized (Marvier & Smith 1997; Guerra *et al.* 2018). In our study, we observed that the preference by hosts at species level was sharply different between fragments. These differences are likely related to the successional stages of the fragments. In Fragment 1, with a more recent disturbance history, and where pioneer trees are more abundant (Cassola 2008; Jorge & Pereira 2015), the parasite frequency in the tree species *C. floribundus* was markedly higher than in liana species, though these lianas are also abundant in Fragment 1. Pioneer species tend to dominate communities in early successional stages, and they are replaced by other tree species in a few years, once canopy closure leads to the decline of shade-intolerant species (Brokaw & Scheiner 1989; Tabarelli & Mantovani 1999). Liana species are more shade tolerant than pioneer trees and continue to develop even under closed canopies (Engel *et al.* 1998). In Fragment 2, anthropogenic disturbances ceased earlier and pioneer trees, including the preferential host *C. floribundus*, should have become rarer than in Fragment 1. Due to the decline of the preferential hosts, *S. fungiforme* became also less abundant, and parasitized liana individuals, as an alternative source of resources to stay alive.

The occurrence of preferred hosts of parasite species in early successional forests reinforces their conservation value, aiming at protecting parasite species and their habitats (Windsor 1995). On the other hand, parasite species conservation relies on the persistence of host species, especially of the preferential hosts, which can improve the survival of parasitic species and which are essential to their conservation (Marvier & Smith 1997). The existence of a mosaic of secondary forests and late successional forests combined with the maintenance of gap dynamics in mature forests are crucial to the persistence of *C. floribundus* populations in seasonal tropical forests. These tree populations, in their turn, ensure the conditions necessary for the persistence of *S. fungiforme*, preserving a wider interaction web based on provisioning resources to fauna by parasite species during periods of food scarcity.

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