Multiple-scale spatial distribution of the fungal epiphyll *Scolecopeltidium* on *Trichilia* spp. in two lowland moist tropical forests

Gregory S. Gilbert, Nicole Talaro, Christine A. Howell, and Amy Symstad

Abstract: The leaf-inhabiting fungus *Scolecopeltidium mayteni* (Micropeltaceae) is common on *Trichilia tuberculata* in lowland tropical forests on Barro Colorado Island, Panama, and on *Trichilia moritzii* in Corcovado National Park, Costa Rica. The sexual reproductive structures (ascomata) of the fungus have a clumped or random distribution on leaflet surfaces. The density of ascomata correlates well with the density of hyphae on the leaf surface and is a good indicator of the intensity of fungal colonization. Most of the variability in colonization is at a leaf-to-leaf level rather than among leaflets or among plants. Intensity of fungal colonization is directly related to the light environment of the leaflet or plant, but not to the density of hosts. The *Scolecopeltidium*–*Trichilia* system is well suited for studies on ecological factors affecting host–fungal symbioses in natural plant communities.

Key words: *Trichilia tuberculata*, *Trichilia moritzii*, Loculoascomycete, density dependence, Panama, Costa Rica.

Résumé : Le champignon folicole *Scolecopeltidium mayteni* (Micropeltaceae) est commun sur le *Trichilia tuberculata* dans les forêts des basses terres tropicales de l'Île Barro Colorado, au Panama, et sur le *Trichilia moritzii* dans le parc national de Corcovado, au Costa Rica. Les structures de reproduction sexuelle (ascomata) du champignon forment un amas ou sont distribuées aléatoirement sur les surfaces foliaires. La densité des ascomata est bien corrélée avec la densité des hyphes sur la surface de la feuille, et est un bon indicateur de l'intensité de la colonisation fongique. La majeure partie de la variabilité de la colonisation se situe au niveau feuille-à-feuille, plutôt qu'entre les feuilles ou entre les plantes. L'intensité de la colonisation fongique est directement reliée à l'environnement lumineux de la foliole sur la plante, mais pas à la densité des hôtes. Le système *Scolecopeltidium*–*Trichilia* se prête bien aux études sur les facteurs écologiques qui affectent les symbioses hôte–champignon dans les communautés végétales naturelles.

Mots clés : *Trichilia tuberculatum*, *Trichilia moritzii*, Loculoascomycètes, dépendance de la densité, Panama, Costa Rica.
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Introduction

Fungi that live in symbioses with plants, whether as mutualists, commensals, or parasites, are important components of natural communities (Alexander 1992; Augspurger 1983; Clay 1988; Connell and Lowman 1989; Gilbert et al. 1994; Lodge et al. 1996; Wills and Keighery 1994). Understanding how the spatial distribution of one symbiont relates to the distribution of its partner provides important keys to identifying the ecological determinants and effects of the symbiosis. Host abundance, geographic barriers to fungal dispersal, genetic variability in the host or fungal populations, and the physical environment can all be important in determining the geographic distribution and the ecological outcome of plant–fungal symbioses. In some cases, a disease produced through association with fungal pathogens could restrict the distribution of the plant host. In other situations the fungus might be constrained to a subset of the ecological conditions that are suitable for the plant, limiting the distribution of the fungus, and thus of the symbiosis, to a portion of the range of the host.

There have been few studies on the ecological constraints to relationships between fungal symbionts and their plant hosts in natural communities. Nevertheless, several important factors regulating disease incidence have been demonstrated for plant diseases in the tropical moist forest of Barro Colorado Island (BCI), Panama. Damping-off disease of seedlings of the tree *Platypodium elegans* (Fabaceae) and a canker disease of saplings of *Ocotea whitei* (Lauraceae) were more severe at high host densities than low and among individuals close to conspecific adults than far away (Augspurger 1983; Augspurger and Kelly 1984; Gilbert et al. 1994). For both *Platypodium* and *Tachigali versicolor* (Fabaceae), offspring that were dispersed into light gaps (canopy openings) suffered substantially less damping-off than seedlings in the shade (Augspurger 1984; Kitajima and Augspurger 1989), with the effect of light gaps being strongest at high host densities. Botryosphaeria canker on *Tetragastris panamensis* (Gilbert and DeSteven 1996) can have severe effects on host survival, and disease development is associated with drought conditions. Elsewhere in

G.S. Gilbert[1] **and N. Talaro.** Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, Republic of Panamá.
C.A. Howell. Division of Biological Sciences, University of Missouri, Columbia, MO 65211, U.S.A.
A. Symstad. Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, U.S.A.

[1] Author to whom all correspondence should be addressed.
Present address: Department of Environmental Science, Policy, and Management, 151 Hilgard Hall, MC 3110, University of California, Berkeley, CA 94720, U.S.A.
e-mail: ggilbert@nature.berkeley.edu

Panama (in a seasonally dry forest), various foliar diseases showed an assortment of patterns of vertical stratification within individual trees related to differences in exposure to the sun (Gilbert 1995). In each of these cases the realized distribution of the plant—fungus association was an environmentally defined subset of the distribution of the host.

Those plant—fungus symbioses in which the fungus requires the host for reproduction but the host experiences little benefit or cost offer unique opportunities for investigating the spatial distribution of fungal symbionts in natural communities. In such cases the distribution of the fungus within the host distribution is uncoupled from effects of the fungus on the host (i.e., through reduced or increased host survival).

In the lowland tropical forest on Barro Colorado Island, Panama, the Loculoascomycete fungus *Scolecopeltidium mayteni* (Micropeltaceae) is common enough on leaves of *Trichilia tuberculata* (Meliaceae) that the presence of black dots on the upper leaf surface is often considered a useful trait in identification of the plant. The black dots are really the shield-shaped sexual reproductive structures (ascomata) of the fungus. Superficially similar ascomata can be found on other host plants on BCI, but in a survey of dozens of samples of similar fungi from other plant species, this fungus was never found on any host other than *T. tuberculata* (G.S. Gilbert, personal observation). Scanning electron microscopy showed that leaves with ascomata are covered by a superficial network of mycelium that may form a nearly continuous layer of hyphae on the leaf surface (G.S. Gilbert, personal observation). There are no apparent negative or positive effects of *Scolecopeltidium* on the host plant.

In this paper we describe the distribution of *Scolecopeltidium mayteni* in two seasonal lowland tropical forests: on leaves of juveniles of the common, shade-tolerant, canopy tree *Trichilia tuberculata* on Barro Colorado Island and on leaves of *Trichilia moritzii* in Corcovado National Park, Costa Rica. We explore the distribution of the fungus at several spatial scales, from within individual leaflets to across a host population, and investigate the importance of host density and the light environment on the host—fungus association. We determine the relationship between density of hyphae on the leaf surface and ascomata production to evaluate whether ascomatal density is a good indicator of the intensity of fungal colonization on a leaflet. We then test whether the ascomata are randomly dispersed, clumped (suggesting preferred sites or poor dissemination), or regularly dispersed (suggesting competition for space or nutrients in reproduction), within individual leaflets. We also describe the patterns of colonization among leaflets, leaves, and vertical strata within individual host plants. We use information from these intensive studies of the distribution of ascomata to design an efficient sampling strategy to assess the distribution of *Scolecopeltidium* across populations of plants and employ this strategy to ask whether fungal incidence was host-density dependent and whether light gaps influence the association.

Materials and methods

Study sites

Barro Colorado Island is a 1500-ha biological reserve in Lake Gatun (approx. 100 m above sea level (a.s.l.)), part of the Panama Canal, Republic of Panama. The Smithsonian Tropical Research Institute administers the research facilities on the island. The forest is a seasonal moist tropical forest that receives an average of 2600 mm of rain per year, punctuated by a 4-month dry season from January through April (Windsor 1990). The Corcovado National Park (CNP) is on the Osa Peninsula, Puntarenas Province, Costa Rica. The forest surrounding the Sirena Biological Station, where part of this study was conducted, is within 2 km of the Pacific coast and less than 100 m a.s.l. It receives approximately 4000 mm of rain per year (Coen 1983), with a seasonality similar to that of BCI.

Study organisms

Trichilia tuberculata (Meliaceae) is the most common canopy tree in the old-growth forest on BCI (Condit et al. 1992). It has compound leaves with five to nine alternate leaflets, including one terminal leaflet. New leaves are not restricted to the top of juveniles; they are produced both at the top of the plant and from branches all along the trunk (G.S. Gilbert, personal observation). Saplings are shade tolerant and survive well in the forest understory. Juveniles of the very similar *T. moritzii* are frequently found in the understory of secondary forests near the Sirena Station in CNP (G.S. Gilbert, personal observation; Hartshorn and Poveda 1983) but are much less common than is *T. tuberculata* on BCI.

Don Reynolds of the Natural History Museum, Los Angeles, Calif., kindly identified collections of the fungus from BCI as *Scolecopeltidium mayteni* (Micropeltaceae) (Batista 1959), previously collected in Brazil on *Maytenus rigida* (Celestraceae). Reynolds cautions, however, that the Micropeltaceae are in need of revision, and that species delimitation are arbitrary (D. Reynolds, personal communication). Numerous attempts to grow the fungus in pure culture have been unsuccessful, although it is relatively easy to collect large numbers of ascospores. Fungi in this family are widespread and grow epiphytically on leaves and other plant parts (Batista 1959).

Distribution within leaflets

We tested whether ascomata density reflected the extent of fungal mycelium on the leaflet surface by sticking double-sided tape against the upper surface of a leaflet and then placing the tape hyphal-side-up onto a microscope slide, a method modified from Langvad (1980). Mounts were stained with methyl blue and examined at 400× with a compound microscope. For each leaflet, we counted the number of hyphae intersecting five 240-μm line transects. The mean number of intersections per line is the hyphal density index for the leaflet. We determined the density of ascomata on each leaflet by counting all ascomata and measuring the area of a paper tracing of the leaflet on a LI-COR LI-3100 leaf area meter (LI-COR, Inc., Lincoln, Neb.). In all, 219 leaflets (10 randomly selected leaflets from randomly selected leaves from each of 22 plants, minus one lost leaflet tracing) were measured. Plants ranged in size from 1.0 to 3.4 m in height, and were less than 3 cm DBH (diameter at breast height; at 1.3 m). This study was carried out at the CNP site in early March 1994. We used a mixed-model analysis for the correlation between hyphal ascomatal density, accounting for plant-to-plant variability, using SAS (version 6, SAS Institute Inc., Cary, N.C.).

Throughout the remaining portions of this study, we used the density of ascomata on the leaflet surface as a measure of the intensity of colonization. In March 1993 on BCI, we examined whether ascomata were clumped, random, or regularly dispersed over the surface of randomly selected individual leaflets, by overlaying an acetate grid on the leaflet, and determining the number of ascomata in all quadrats of 22.1 and 88.4 mm^2 on the leaflets ($n = 27$ leaflets). We excluded those quadrats that overlapped the edge of the leaflet. We used Morisita's index:

$$[1] \quad I_\delta = \frac{n[\Sigma x(x-1)]}{\Sigma x(\Sigma x - 1)}$$

where x is the count in each quadrat, and n is the number of quadrats, to compare the observed frequency distribution to that expected for a random distribution (Campbell and Madden 1990). We considered that I_δ indicated a distribution significantly different from random ($I_\delta = 1$) when

[2] $\quad I_\delta^* = I_\delta(\Sigma x - 1) + n - \Sigma x$

was outside the appropriate significance level ($\alpha = 0.05$) of chi-square for $n - 1$ degrees of freedom.

Distribution within plants

On two sapling-sized individuals of *Trichilia tuberculata* on BCI, we determined, for each leaflet on the entire plant, the number of ascomata and the area of existing leaf tissue. In CNP, we measured ascomatal density on 5 leaflets on each of 10 randomly selected leaves from 5 individuals.

To determine whether colonization severity varied on a plant, leaf, or leaflet basis, we determined how the variance of density of ascomata was partitioned between leaflets (error), leaves, and plants by nested ANOVA (Snedecor and Cochran 1989). Analyses were conducted separately for BCI and CNP. Ascomatal densities were square-root transformed to meet assumptions of homogeneity of variance.

To determine whether density of ascomata was related to leaflet position within leaves, we performed a mixed-model analysis of the effect of leaflet position within leaves, with leaflet position 1 being closest to the leaf base (134 leaflets on 22 leaves and 392 leaflets on 53 leaves, respectively, for the same two BCI individuals).

Additionally, for 50 individuals (between 1.3 and 4.9 m tall, each at least 20 m from a trail) selected haphazardly from across BCI, we determined the density of ascomata on 1 leaflet from each of 10 randomly selected leaves each from the top, middle, and bottom thirds of the tree (30 leaflets per plant). We developed this sampling strategy through simulations using the data collected from the two BCI individuals for which the total ascomatal density was known. For each plant we randomly sampled a range of proportions of total leaves (4–87%), and one, two, or three randomly selected leaflets per leaf. Each random sampling was performed 20 times. There was no benefit from sampling more than one leaflet per leaf (based on approximation to the true mean for the plant and on changes in the standard error of the mean) nor for sampling beyond 18% of the total leaves (20 leaves on the large plant 2). Subsequently, we included vertical stratification in the sampling to account for the observed differences in ascomatal density among different strata of the plants. Through this simulation procedure we found sampling 1 leaflet for each of 30 leaves (in all cases more than 18% of the total leaves; divided equally among top, middle, and bottom thirds of the plant) to be a rapid and robust estimator of ascomatal density for each section and for the plant overall. We tested for differences in ascomata density among the three vertical positions using Fisher's protected least significant difference (Snedecor and Cochran 1989), with the ANOVA treating trees as blocks and the mean densities of ascomata among leaflets within a section of an individual plant as the experimental unit.

Distribution within the population and effect of host density

We used the data collected from the 50 individuals from BCI described above to determine how ascomata density varied throughout the host population. We estimated the mean density for each tree by calculating the mean of the means of each section. To determine whether there was an effect of host density on the intensity of fungal colonization, we also measured the distance to the nearest conspecific individual (an inverse measure of host density), and counted the number of individuals within 5- and 10-m radii around the focal plant.

Effect of canopy openness on fungal incidence

To investigate relationships between the light environment and fungal colonization, we took hemispherical canopy photographs from immediately above the top of 19 of the above 50 BCI individuals (chosen at random). These photographs were analyzed as described by Becker et al. (1989) to determine percentage of open canopy and global radiation over the course of a year. In CNP, we took ascomatal density measurements and canopy openness measurements over 22 individuals using a hand-held spherical canopy densiometer. For 17 of the plants, we calculated the mean ascomatal density for the plant from one randomly chosen leaflet from each of 10 leaves per plant (10 leaflets per plant); the remaining five plants were those described under the Distribution within plants section, and means were calculated from 50 leaflets. We compared the mean density of ascomata per plant to the light measurements by least-squares linear regression analysis (Snedecor and Cochran 1989). Regression lines for the two sites were compared according to Mead and Curnow (1983).

Results

Morphology and habit of *Scolecopeltidium* on *Trichilia tuberculata*

Mature leaves of *Trichilia tuberculata* are normally shiny but take on a matte appearance when colonized by *Scolecopeltidium*. The black, shield-shaped ascomata develop from a dense mycelium one cell layer thick, which grows across the upper surface of the leaf but apparently does not penetrate host tissues. Mycelium may cover the entire leaflet surface. Each ascus contains eight multicelled hyaline ascospores of variable size and cell number. Ascomata were not found on very young leaves. *Scolecopeltidium* on *T. moritzii* appeared identical to that on *T. tuberculata*.
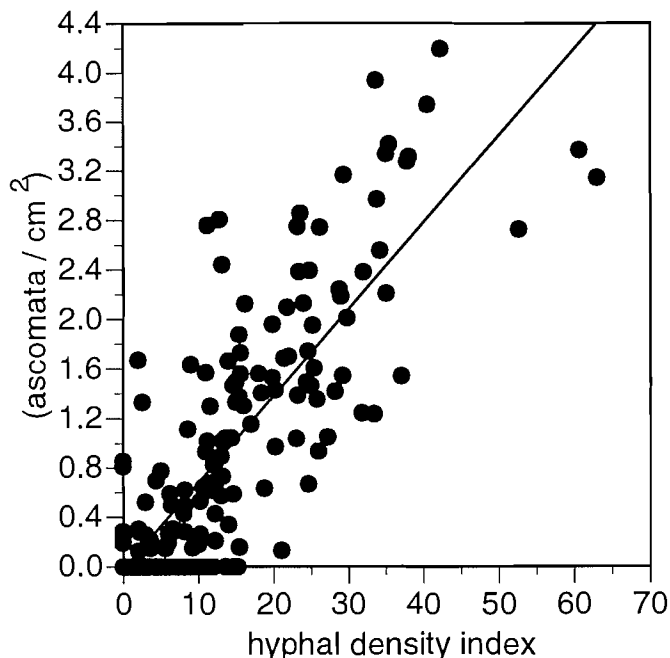
Distribution within leaflets

Ascomatal density was very strongly correlated with hyphal density within leaflets (Fig. 1) (effect of hyphal density: $R^2 = 0.64$, $F_{1,196} = 265.5$, $P = 0.0001$; effect of plant: $F_{21,196} = 3.65$, $P = 0.0001$), indicating that ascomatal density (an easily measured parameter) could be used as a surrogate for fungal density. Ascomata were significantly clumped for 17 of 27 leaflets examined as determined by values of Morisita's index significantly different from 1.0 ($P \leq 0.05$ for 2 leaflets; $P \leq 0.001$ for 15 leaflets). However, the distribution of ascomata was not significantly different from random for 10 of 27 leaflets. Results were qualitatively similar at both quadrat sizes. This suggests preferred sites within leaflets for fungal colonization or growth.

Distribution within plants

To test whether there was an effect on ascomatal density of position of the leaflet within a leaf (i.e., whether more exposed distal leaflets had higher levels of colonization than proximal leaflets), we regressed ascomatal density against the leaflet position within leaves on two plants. We found no significant relationship between ascomatal density and leaflet position for either plant ($F_{1,112} = 0.41$, $P = 0.52$ and $F_{1,224} = 1.73$, $P = 0.19$, respectively). Leaf effect was significant in both cases ($F_{21,112} = 0.41$, $P = 0.52$ and $F_{52,224} = 1.73$, $P = 0.19$).

For two plants on BCI and five at CNP we determined how the variance of ascomatal density was partitioned among plants, leaves, and leaflets. In each case, differences among leaves were significant, but differences among plants were

Fig. 1. Relationship between density of ascomata and density of fungal hyphae for *Scolecopeltidium mayteni* on leaflet surfaces of *Trichilia moritzii* in Corcovado National Park. Regression line represents $(ascomata/cm^2)^{0.5} = -0.025 + 0.07(hyphal density)$, $R^2 = 0.71$.


Fig. 2. Density of ascomata of *Scolecopeltidium* on *Trichilia tuberculata* as a function of distance to nearest conspecific plant. Of the 50 plants surveyed, 6 had no conspecific within a 30-m radius (those points not shown).

significant only in CNP (Table 1). In both sites, leaf-to-leaf variance accounted for the greatest amount of total variance (79% on BCI, 48% in CNP). The leaflet-position and nested ANOVA analyses indicate that most of the variability in ascomatal density occurs at the leaf-to-leaf level and that choice of particular leaflets within a leaf will not have a large influence on the overall density estimate for the leaf.

There was, however, a significant effect of vertical position within the plant on ascomatal density. There were higher densities of ascomata in the top (0.47 ± 0.05 ascomata/cm²; mean SE) and middle (0.44 ± 0.07) sections than in the bottom (0.32 ± 0.06) third of 50 BCI individuals (Fisher's protected least significant difference, $P \leq 0.05$). Analysis of variance showed a significant block effect of trees ($F_{49,98} = 2.07$, $P = 0.0013$), as well as a significant vertical section effect ($F_{2,98} = 4.48$, $P = 0.014$). This indicated that a stratified sampling strategy is appropriate for estimating fungal colonization levels of whole trees.

Distribution within the population and effect of host density

We used a within-tree stratified sampling strategy (1 leaflet for each of 10 leaves from each of 3 vertical sections of each plant) to assess the distribution of colonization by *Scolecopeltidium* throughout the population of *T. tuberculata* juveniles on BCI. Mean ascomatal density for the population sample of 50 individuals was 0.41 ± 0.42 ascomata/cm² (mean ± SD). The distribution of means indicated that most individuals have very low densities of ascomata (46% of samples had a mean density <0.30 ascomata/cm²), with a long tail to higher densities of as much as 1.2 ascomata/cm². We found only one individual with no ascomata.
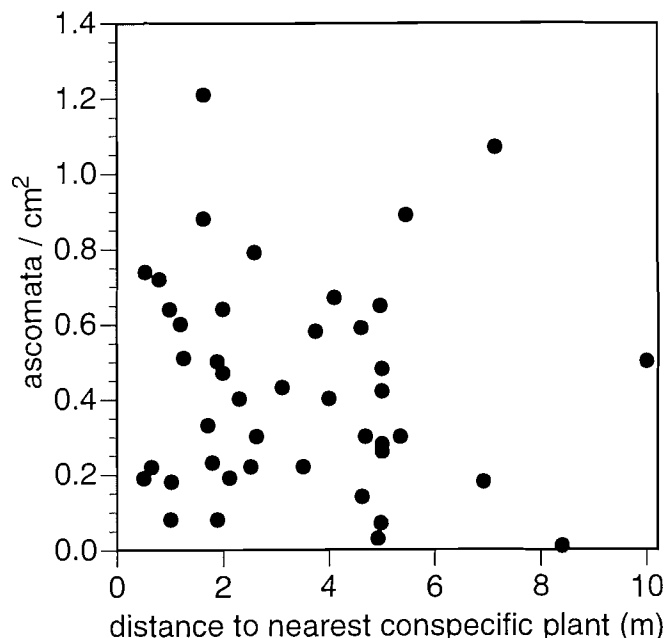
Table 1. Nested ANOVA to partition variance of ascomata density among plants, leaves, and leaflets of *Trichilia tuberculata* on Barro Colorado Island, Panama and *T. moritzii* in Corcovado National Park, Costa Rica.

Site	Source	df	SS	F	P	Percentage of total variance
BCI	Plant	1	0.1	0.02	>0.5	0
	Leaf	73	182.6	21.1	0.0001	79
	Leaflet	338	40.1			21
	Total	412	222.7			100
CNP	Plant	4	70.1	6.8	0.0002	31
	Leaf	45	115.1	12.2	0.0001	48
	Leaflet	200	42.1			21
	Total	249	227.3			100

We found no relationship between mean ascomatal density for a plant and the distance to its nearest conspecific neighbor (Fig. 2) nor with the number of conspecific hosts in 5- or 10-m radii (data not shown). Ascomatal density for six host individuals for which we could not find a conspecific host within 30 m ranged from 0.02 to 0.98 ascomata/cm² (mean = 0.33) with a distribution similar to the remaining plants, so their exclusion from Fig. 2 does not affect the conclusion that there is no evidence for density dependence in fungal colonization.

Effect of canopy openness on fungal colonization

There were strong effects of canopy openness on the density of ascomata both at BCI and CNP. The juveniles of *T. tuberculata* that we haphazardly selected for study on BCI were found in a fairly narrow range of canopy openness; nevertheless, there was a striking positive relationship between asco-

Fig. 3. Mean density of ascomata of *Scolecopeltidium* in the top, middle, and bottom thirds of juveniles of *Trichilia tuberculata* on Barro Colorado Island, as a function of canopy openness. The regression equation for the top section is density = 0.488 + 0.412 log(% open), $F_{1,17} = 17.67$, $P = 0.0006$, $R^2 = 0.51$. Slopes from the regressions for the middle ($P = 0.78$) and bottom ($P = 0.07$) sections were not significantly different from zero. Percent canopy openness was determined using hemispherical canopy photographs.
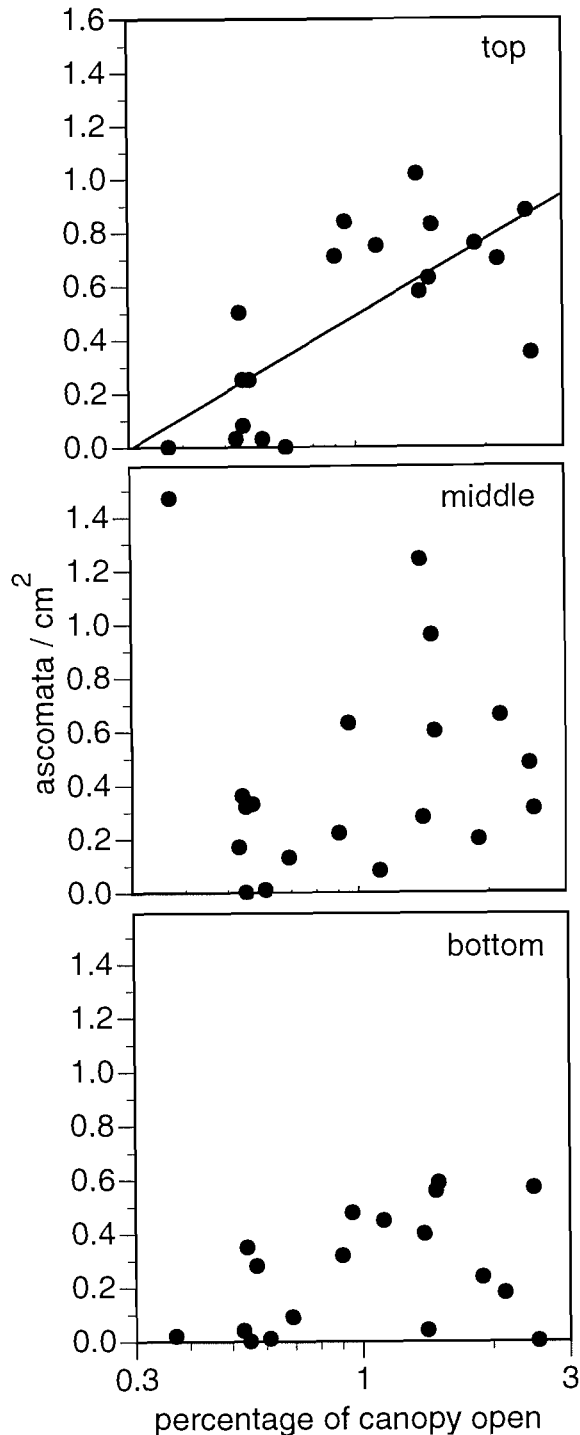
Fig. 4. Mean density of ascomata of *Scolecopeltidium* on leaflets of juveniles of *Trichilia tuberculata* on Barro Colorado Island (BCI) (○) and on *T. moritzii* in Corcovado National Park (CNP) (●), as a function of forest canopy openness above the tree. Canopy openness was measured using hemispherical photos at BCI and with a hand-held spherical densiometer at CNP. The solid line represents the regression using the combined data ($y = 0.65 + 0.62$ log x, $F_{1,39} = 43.7$, $P \leq 0.0001$, $R^2 = 0.52$), where y is (ascomata/cm^2)0.5 and x is percent canopy open. The broken line includes only BCI data ($y = 0.58 + 0.45$ log x, $F_{1,17} = 5.53$, $P \leq 0.031$, $R^2 = 0.20$), and the dotted line only CNP data ($y = 0.78 + 0.53$ log x, $F_{1,20} = 11.7$, $P \leq 0.003$, $R^2 = 0.34$).
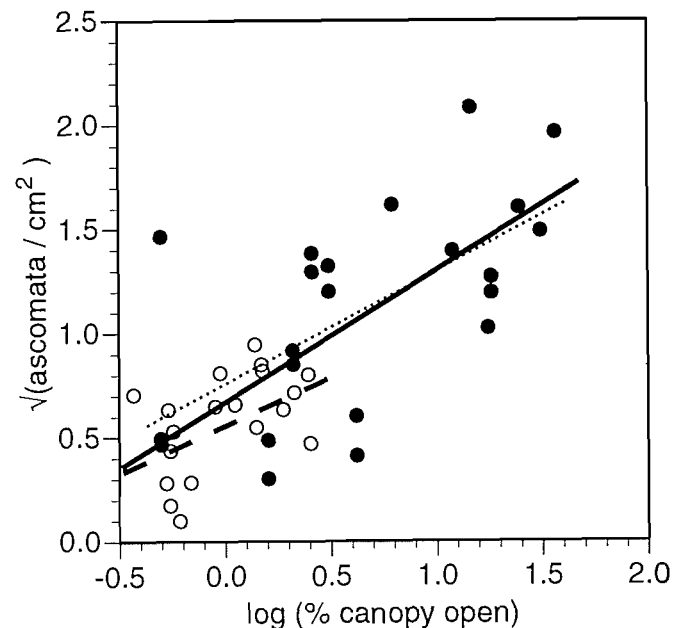
matal density and openness for leaflets in the top third of the plant, which are most likely to receive direct radiation (Fig. 3). Leaflets in the middle and bottom sections of the plants did not show such a response ($P > 0.05$) (Fig. 3). When the mean ascomatal density for entire plants was analyzed, there was a strong positive relationship between fungal colonization and canopy openness for both sites (Fig. 4). Plants were found in a much broader range of light environments in CNP than on BCI, but there was no significant difference between the two regressions ($F_{2,37} = 1.24$, $P > 0.05$), indicating that a single regression line for the two sites is appropriate.

Discussion

Scolecopeltidium is present on nearly all the individuals of *Trichilia* found both on Barro Colorado Island in Panama and in Corcovado National Park in Costa Rica. Its abundance in both forests, despite an apparently restricted host range within the communities of the forests studied, suggests a stable, widespread symbiosis. Although most host individuals are affected, the intensity of colonization varies widely among plants within a population and among leaves and leaflets within a host individual. The close association between density

of ascomata (which is easily measured) and hyphal density on the leaf surface (which requires slow microscope work) makes this an excellent system for studies on ecological factors affecting fungal distribution.

Ascomata production on the surface of individual leaflets varies from randomly distributed to clumped. This suggests that there are particular sites on leaflets more or less conducive to fungal colonization, growth, or reproduction. Such sites on leaves may retain water longer after a rain than others because of the wavy nature of the leaflets. The importance of such microsite variation in leaf water retention and its importance in microbial colonization of tropical leaves by microorganisms was postulated originally by Ruinen (1961). Ascospores ejected through the central pore of an ascoma during or before a rain would be easily dispersed to lower leaves during rain throughfall, and small puddles of water on leaves may lead to localized colonization. On the other hand, more rapid drying of leaves may facilitate colonization of leaves once propagules have immigrated. Ascospore production on BCI is very limited during the wettest part of the rainy season (October−November), but extensive around the time of the first rains (March−April) (G.S. Gilbert, personal observation). This may suggest that the fungus is better suited to slightly drier conditions.

Since nearly all individuals of *T. tuberculata* and *T. moritzii* are infected with *Scolecopeltidium*, one would expect that all leaves encounter spores of the fungus throughout their lifetimes. The strong leaf-to-leaf variability (compared with within-leaf variability) of colonization intensity suggests that leaf phenology may be key to the colonization process. One possibility is that there may be only a narrow window during the development of a leaf when it is susceptible to colonization. If spores are abundant during that period, we would expect most of the leaflets in a leaf to become colonized. If, on the other hand, spores were scarce, all leaflets may pass through the susceptible period unaffected. Such a scenario would lead to low leaflet-to-leaflet variability, and greater leaf-to-leaf variability, consistent with our observations.

This pattern of variability is fortuitous for rapidly assessing colonization levels in whole plants. Assessing the ascomatal density on one leaflet gives most of the information available from an entire leaf, and a limited number of leaflets sampled from three vertical strata provides an adequate estimate of overall colonization level for studies on the influence of many ecological factors on the incidence and extent of colonization.

In one such study, we found that the light environment appears to be an important determinant for *Scolecopeltidium* densities and may be a factor in the observed leaf-to-leaf based variation. Within plants, those leaves at the top of the plant, and thus least susceptible to self-shading, consistently have the more intense colonization. Additionally, the higher the light levels experienced by an individual plant, the more extensive the fungal colonization. Differences in light environments might be correlated with differences in the impact of dew, rain, or drip from canopy leaves; such differences in water quality and quantity may interact strongly with the light environment to determine success and extent of colonization (Ruinen 1961).

Although host density is very often positively correlated with disease severity (Burdon and Chilvers 1982; Gilbert

et al. 1994), we found no evidence for density dependence in colonization by *Scolecopeltidium*. This may indicate that the environment is functionally saturated with propagules of the fungus, at least at certain times of the year, and fungal dispersal is not a limiting factor in the incidence of the symbiosis.

Acknowledgments

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