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Myxomycetes associated with bryophyte mats in San Ramón, Costa Rica

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Abstract: Myxomycete-bryophyte associations have been studied mostly in temperate regions of the world. Data from tropical regions are much more limited. The interesting landscape configuration of the San Ramón area in Costa Rica, within the context of the Sierra de Tilarán, allowed an investigation of this ecological association. Results from the present study suggested that moisture could be relevant for generating new data on the associatons of myxomycetes associated with bryophytes. Since available information does not yet allow the testing of interesting ecological questions, simple experiments such as this one facilitate the accumulation of relevant information for future evaluation of pertinent biological hypotheses relating to natural microhabitats.

Keywords: ecology, microhabitats, mosses, tropical forests

Introduction

The association between the fruiting bodies of myxomycetes and bryophytes has been studied during the several decades (e.g., Stephenson and Studlar 1985; Ing 1994). Based on data from these studies, it has been suggested that some myxomycetes could be considered “muscicolous” or “bryophylous” (Ing 1994), and there is general agreement that bryophytes represent one substrate that should be considered when assessgin the biodiversity or ecological patterns of myxomycetes.

The myxomycete-bryophyte relationship, however, is not fully understood. It is clear that bryophytes provide exposed surfaces that are convenient for myxomycete sporulation (Stephenson and Studlar 1985), but the underlying mechanisms explaining such association are still enigmatic. Ing (1994), suggested that myxomycetes could grow on bryophytes as a product of the high nitrogen content present in bryophyte mats usually co-occurring with nitrogen-fixing cyanobacteria, but Dudka and Romanenko (2006) concluded, based on an experiment they had carried out, that the relationship between myxomycetes and bryophytes is strictly spatial and not trophic.

Bryophytes are effective at trapping airborne spores of myxomycetes (Stephenson and Rojas 2020), and epiphytic bryophytes provide an opportunity for both airborne spores and corticolous myxomycetes to develop under more favourable conditions (de Haan 2014). Interestingly, even though bryophytes are microhabitats for myxomycetes in temperate forests, their species richness and abundance are relatively low (Stephenson and Studlar 1985; Stephenson and Stephenson 2022). The strength and direction of these indicators in tropical forests are still largely undocumented, and the limited study presented herein was carried out to increase this type of information. The presence of sporocarps of few species of myxomycetes, such a *Barbeyella minutissima*, have been strongly linked with the presence of bryophyte mats (Stephenson and Studlar 1985), but similar associations in tropical forests are unknown.

The area of San Ramón, in the westernmost part of the "Central Valley" in Costa Rica offers the conditions necessary to study the myxomycete-bryophyte association in a tropical landscape. This area has a mild climate with an average annual temperature of 21°C and an accumulated precipitation of about 3000 mm/year. The presence of the Sierra de Tilarán mountains shaping the continental divide creates two different microclimatic conditions as well, with a dryer seasonal side on the Pacific slope and a moister non-seasonal side on the Caribbean one. In this context, bryophytes are associated with orographic clouds of variable effect in the former and with moist east trade winds of constant effect in the latter.

Materials and methods

This study was carried out in the easternmost section of the Sierra de Tilarán in Costa Rica, a low elevation mountainous area, between 700-1500 m in elevation, located in the central part of the country. The nearest largest city (San Ramón) in this section of Costa Rica provides the colloquial designation used for the entire general area. Due to the presence of the continental divide, which brings plenty of moisture, the San Ramón area is normally foggy and rainy, with slightly lower temperatures than neighbouring areas in lower elevations. Such climatic characteristics are normally associated with an abundance of bryophytes growing on trees, logs, rocks, and ground (Fig. 1).

For this project, two sampling locations were selected, one on either side of the continental divide. The first location corresponded to a Caribbean slope forest near Los Lagos, on the road to the Alberto Manuel Brenes Biological Reserve (abbreviated as SR1, 10.2336, -84.5335, 822 m) and the second location corresponded to a Pacific slope forest near the Valle de Los Quetzales Nature Reserve (abbreviated as SR2, 10.1482, -84.5825, 1524 m). Both places are located within the San Ramón County and were visited during the beginning of the dry season on 11 December 2021.

At each of the two selected locations, one large sample of bryophytes was collected separately from the base of living trees, the ground, and the surface of decayed logs. Each of the three samples corresponded to a mixture of the respective material obtained from different sampling points, trees or logs. In each case, enough material was collected to prepare at least ten moist chamber cultures, but in one instance, there was only enough for eight cultures. In all cases, however, the material was placed on filter paper inside a Petri dish and the moist chamber protocol described by Stephenson and Stempen (1994) was used to study the presence of fruiting bodies of myxomycetes associated with the bryophytes.

When fruiting bodies were detected, they were extracted from the Petri dish and glued into a pasteboard box for storage. These vouchers were deposited at the herbarium of the University of Arkansas (UARKM) using the nomenclature provided by Lado (2005-2022). A two-way ANOVA was used to test differences in pH values by collecting location and bryophyte type. In this case, a P=0.05 was used to establish significant differences.

Figure 1. Map of Costa Rica (left) showing primary administrative divisions, the two sampling locations of this study in the San Ramón area and the continental divide (red line). The images on the right correspond to the general aspect of the surveyed forests.

Results

A total of 63 moist chambers were prepared with the material collected in this project. From these, 28 (~45%) moist chambers used material from SR1 and 35 (~55%) from SR2. In all cases, except for the bryophytes from the ground at SR1, at least 10 moist chambers per sample were set up. Overall, 32 samples of bryophytes, equivalent to 50.8% of the total collecting effort generated positive results of myxomycetes. From these, 12 samples yielded fruiting bodies and the other 20 produced only plasmodia. The samples from SR1 were more productive than those from SR2 in terms of the number of positive moist chambers, recorded plasmodia, observed sporocarps, and recorded species (Table 1).

Table 1. Summarized results of the present study arranged by collecting location. The highest values are shown in bold.

Effort and productivity	**Collecting location**	
	SR1 (Caribbean)	**SR2 (Pacific)**
Total number of moist chambers	28	**35**
Number of positive moist chambers	**20 (71.4%)**	12 (34.3%)
Number of non-fruiting plasmodia	**11 (39.3%)**	9 (25.7%)
Number of sporocarps of myxomycetes	**11 (39.3%)**	3 (8.6%)
Number of recorded species	**6 (All recorded species)**	1 (only *Arcyria cinerea*)

The six species of myxomycetes identified in this project were *Arcyria cinerea*, *Didymium iridis*, *D. squamulosum*, *Diderma effusum*, *Di. Hemisphaericum*, and *Lamproderma* sp. Of these, all of them were recorded in SR1 and only the first one was recorded in SR2. The pH values associated with the moist chambers showed that *A. cinerea* formed sporocaps in the most acidic microhabitats (average pH = 5.8 ± 0.5) and both *D. difforme* and *Di. hemisphaericum* were associated with the most neutral pH values (average pH = 6.6 ± 0.0 and 6.6 ± 0.4, respectively). Interestingly, the pH differed among the type of bryophyte studied ($F(2,59)=8.1$, $P = 0.001$) with the material from the ground showing the highest values (average pH = 6.4 ± 0.4). The pH of bryophytes from the base of trees or from decayed wood showed lower values (average pH = 5.9 ± 0.4 and pH = 6.0 ± 0.4, respectively). Significant differences in pH values were also observed in the interaction of type of bryophyte and collecting location as well ($F(2,59) = 3.4$, $P = 0.03$).

Associated with the latter, a substantial difference was observed in the number of positive moist chambers and records associated with the three studied types of bryophytes. As observed in Table 2, bryophytes on decayed wood were the most productive, followed by bryophytes from the base of trees. In contrast, bryophytes associated with the ground were the least productive ones. These results were observed for both locations studied herein, but the difference between SR1 and SR2 is that sporocarps provided the differences in the former and non-fruiting plasmodia in the latter.

Table 2. Results of the present study arranged by the type of bryophyte studied in both collecting locations.

Myxomycete record	**Bryophyte type [SR1-SR2]**		
	Base of tree	**Decayed wood**	**Ground**
Arcyria cinerea	1-0	2-3	0-0
Didymium iridis	3-0	0-0	0-0
Didymium squamulosum	0-0	1-0	0-0
Diderma effusum	0-0	1-0	0-0
Diderma hemisphaericum	1-0	0-0	1-0
Lamproderma sp.	0-0	1-0	0-0
Non-fruiting plasmodia	3-4	4-4	4-1
Total number of records	8-4	9-7	5-1

Discussion

As observed by Stephenson and Stephenson (2022), it could be stated that myxomycetes are associated with bryophyte mats in tropical systems, but their species richness and abundance are both low. The percentage of positive moist chambers observed herein (50.8%) is equivalent to the value observed for the temperate forests of southwestern Virginia in the United States (49%). Also, the recorded number of species is the same in the two cases, but only *A. cinerea* and *Di. effusum* were found in both forest types. All other recorded species in both studies were found only in the respective location. With the available information, the mean value of the pH recorded for byrophyte mats with myxomycetes is higher in temperate areas ([Stephenson and Stephenson 2022], 7.5) than in tropical ones (this study, 6.1). Such differences in the acidity of substrates could have influenced the assemblage of species present.

Based on the results, the bryophyte samples from SR1, the collecting location on the Caribbean side of the continental divide, were more productive at multiple levels. This observation could have been associated with differences in bryophyte species between SR1 and SR2, but in the present study, such identifications were not carried out. However, based on previous results from other researchers and the incidental co-ocurrence of myxomycetes and bryophytes in a number of ecological situations, it seems more likely that moisture could have been the key factor accounting for differences among collecting locations (see Glime 2019 for a similar conclusion on a through review of the association). The difference between SR1 and SR2 is that moisture is much more constant in the former because the moist east trade winds are constantly impacting the Caribbean side of the Sierra de Tilarán, whereas moisture in SR1 comes in the form of orographic clouds associated with the Pacific coast, and these do not form every day. Stephenson and Rojas (2020) also made the observation that moisture levels associated with a forest in Northwest Arkansas could have influenced an experiment where mosses were used as spore traps, and Stephenson and Stephenson (2022) noted that the moister forests in southwestern Virginia were better for the study of the myxomycete-bryophyte association than more xeric ones in the United States.

The amount of wind exposure, presumably different between SR1 and SR2 could have also played a role in modulating the concentration of available spores or propagules able to colonize spore mats. Such aerodynamic modulation could have also been responsible for the higher productivity of moist chambers associated with non-ground bryophytes, although some microenvironmental conditions of the wood microhabitat (such as the observed differences in pH values) could have also played a role. Since both decayed logs and the base of trees were technically located few centimeters away from the ground, such separation could have allowed for air currents to flow more efficiently and for mosses to be more succeptible to promoters of myxomycete fructification such as wet-dry cycles. Since the present study did not focus on the ecological mechanisms explaining the patterns it would be worthwhile to carry out similar evaluations in the future but with a more thorough quantification of variables that could explain the differences. Also, it is necessary to mention that it is very difficult to determine if the differences recorded herein are attributed to the hypothesized mechanisms (e.g., moisture) or simply to chance alone. Ideally, more than three sites and the mentioned stronger design could be necessary to evaluate if the productivity patterns recorded herein hold up

Glime (2019) reviewed the myxomycete-bryophyte association and concluded that there is not enough information to test a large number of ecological questions relating to it. Realistically, based on the incidental information available, which comes largely from biodiversity rather than ecological assessments, it is true that researchers do not have conclusive evidence to demonstrate any type of ecological association between myxomycetes and bryophytes other than the fact of coexistence in crytogamic niches. In this manner, as discussed earlier, even simple experiments testing aspects such as ecological benefit of either group, bryophyte inhibition of myxomycete sporocarps, microtrophic aspects, and the strength of the association across biomes could generate interesting results to continue evaluating such an interesting relationship.

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