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Cover Photograph: Fruiting bodies of *Physarum melleum*, a colorful myxomycete commonly associated with leaf litter. Photograph © Kim Fleming.

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Steven L. Stephenson*

Abstract - In the lower canopy of lowland tropical rainforests, the system of aerial rhizomorphs produced by certain marasmioid agarics intercepts and holds a considerable amount of litter, mostly in the form of dead leaves. The biodiversity of the assemblage of myxomycetes associated with this aerial litter microhabitat actually appears to be higher than the assemblage associated with ground litter in the same forest. As such, rhizomorph systems clearly influence the distribution and ecology of myxomycetes in rainforests. This ecological association has not been recognized previously by those biologists who study these organisms.

In the lower canopy of lowland tropical rainforests, a number of species of marasmioid agarics often form an intricate system of aerial rhizomorphs (César et al. 2018). Typically, these are members of the genus *Marasmius* (Marasmiaceae) but can also include some species in other genera such as *Crinipellis* (Marasmiaceae) and *Gymnopus* (Omphalotaceae). Such aerial rhizomorphs (Fig. 1) are tough and persistent, typically brown or black (but sometimes white) in color and usually between 0.1 and 1.5 mm in diameter (Snaddon et al. 2012). The system of rhizomorphs intercepts a substantial amount of litter, mostly in the form of dead leaves. Snaddon et al. (2012) calculated that approximately 257 kg of leaf litter per hectare was intercepted and held in a tropical rainforest in Malaysia. This material, which has never been in contact with the ground, is referred to as aerial litter (Schnittler and Stephenson 2000). Aerial rhizomorphs are collected and used as nesting material by certain species of birds (Freymann 2008, Koch et al. 2018, Elliott et al. 2019). In fact, some nests may consist almost entirely of rhizomorphs. Snaddon et al. (2012) reported that the system of aerial rhizomorphs also serves as a microhabitat for certain insects. Field observations in the Neotropics (S.L. Stephenson, unpubl. Data) indicate that this is also the case for various other invertebrates—including arachnids, such as mites (order Acari) and spiders (order Araneae).

Myxomycetes (plasmodial slime molds or myxogastrids) are a group of fungus-like organisms associated with dead plant material in virtually every type of terrestrial ecosystem investigated to date, with approximately 1000 species known worldwide (Lado 2005–2020). The myxomycete life cycle encompasses two very different trophic (feeding) stages: one consisting of uninucleate amoebae, with or without flagella (the term "amoeboflagellate" is used to refer to both types), and the other consisting of a distinctive multinucleate structure, the plasmodium (Martin et al. 1983). Under favorable conditions, the plasmodium gives rise to one or more fruiting bodies containing spores. The fruiting bodies produced by myxomycetes are somewhat suggestive of those produced by higher fungi, although they are considerably smaller—usually no more than 1–2 mm tall.

In tropical rainforest ecosystems, myxomycetes are associated with a number of different microhabitats, including decaying coarse woody debris, woody twigs, lianas, the bark surface of living trees, and both aerial litter and ground litter on the forest floor (Fig. 2). Although the fruiting bodies of myxomycetes can be collected in the field from all of these microhabitats, the use of moist chamber cultures, as they apply to the study

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of myxomycetes, is a much more productive method of studying both types of litter microhabitats. These cultures are prepared and then checked for myxomycetes in the manner described by Stephenson and Stempen (1994).

It has long been recognized that various species of myxomycetes are commonly associated with ground litter (Martin and Alexopoulos 1969, Stephenson 1989), but the fact that these organisms are associated with aerial litter is a more recent discovery (e.g., Schnittler and Stephenson 2000, Black et al. 2004, de Haan 2011). Although only a limited number of comparative studies have been carried out, the aerial litter microhabitat appears to support a higher biodiversity of myxomycetes compared to the ground litter microhabitat in moist tropical forests. For example, Schnittler and Stephenson (2000) reported data for two types of tropical forests—primary and secondary—in Costa Rica. In the primary forest, 137 cultures prepared with samples of ground litter yielded an average of 0.7 species of myxomycetes, whereas 100 cultures prepared with samples of aerial litter produced an average of 1.3 species. For the secondary forest, 45 cultures prepared with ground litter yielded an average of 3.0 species, whereas samples of aerial litter produced an average of 4.5 species. In northern Queensland, Black et al. (2004) found that 92% of 61 cultures prepared with aerial litter yielded myxomycetes, whereas only 55% of 11 cultures prepared with samples of ground litter were positive for these organisms.

Figure 1. Dead leaves trapped by aerial rhizomorphs in a tropical rainforest in the Republic of Cameroon in Central Africa (image courtesy of Todd Elliott).

Figure 2. Fruiting bodies of *Physarum melleum* (top, image courtesy of Kim Fleming) and *Physarum compressum* (bottom, image courtesy of Laurie Leonard), two species of myxomycetes commonly associated with the leaf litter microhabitat in tropical rainforests.

In the types of comparative studies mentioned above, the assemblages of myxomycetes recorded from ground litter and aerial litter usually are comprised of mostly the same species, even though they are typically more abundant in the latter microhabitat. Although it is not uncommon for a particular species of myxomycete to be very abundant in one of the two microhabitats and largely absent from the other, there is no evidence to suggest that some species of myxomycetes are absolutely restricted to either microhabitat (S.L. Stephenson, unpubl. Data). However, this does not discount the possibility that some of the rarely recorded species do display a certain degree of microhabitat specificity.

Schnittler and Stephenson (2000) suggested that the apparent displacement of myxomycetes from the forest floor to aerial microhabitats is related to the differences that exist for environmental moisture levels. Myxomycetes appear to be better adapted to survive under fluctuating moisture conditions (more likely to be found in aerial microhabitats) than under conditions of continuously high moisture levels (more likely to exist on the forest floor). Even exposed to daily rainfall, aerial microhabitats tend to dry out rather quickly, whereas microhabitats on the forest floor are likely to retain at least a film of moisture. Under the latter conditions, the fruiting bodies of myxomycetes are often colonized by filamentous fungi, thus severely restricting successful production and dispersal of spores (Rogerson and Stephenson 1993). Schnittler and Stephenson (2000) indicated that the influence of moisture is suggested by the results of the comparative data they had for Costa Rica. The secondary forests they studied had numerous openings, whereas the sampled primary forests had a closed canopy. The overall drier conditions in the former for both aerial litter and ground litter would be expected to be more favorable for myxomycetes, and the data outlined above appear to reflect this suggestion.

It thus seems apparent that the presence of an aerial network of rhizomorphs clearly influences the distribution and ecology of myxomycetes in the forests in which the former occurs. This association has not been recognized previously by those biologists who study these organisms but actually represents a fascinating subsystem within the tropical rainforest ecosystem.

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