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Occurrence of myxomycetes in the aerial "canopy soil" microhabitat

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Abstract

Myxomycetes (also called plasmodial slime molds or myxogastrids) are now known to occur in the aerial "canopy soil" microhabitat of those forest types (primarily temperate and tropical rain forests) in which this type of microhabitat exists. They appear to be less common than dictyostelid cellular slime mold (dictyostelids) in canopy soil but can be relatively common in some microsites. Reported herein are the first records of myxomycetes from canopy soil in the temperate rain forests of the Southern Hemisphere.

Key words – dictyostelids – ecology – epiphytes – forest ecosystems – myxogastrids

Introduction

The myxomycetes (also called plasmodial slime molds or myxogastrids) are eukaryotic microorganisms usually present and sometimes abundant in terrestrial ecosystems. The myxomycete life cycle encompasses two very different trophic stages, one consisting of uninucleate amoebae, with or without flagella, 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). The spores of the vast majority of myxomycetes range in size from 5 to 15 µm in diameter, with most species producing spores 10 ± 2 µm in diameter. Presumably, the spores are wind-dispersed and complete the life cycle by germinating to produce the uninucleate amoeboflagellate cells. These feed and divide by binary fission to build up large populations in the various microhabitats in which these organisms occur. Ultimately, this stage in the life cycle gives rise to the plasmodium.

Bacteria apparently represent the main food resource for both trophic stages, but plasmodia are also known to feed upon yeasts, algae (including cyanobacteria), and fungal spores and hyphae (Stephenson & Stempen 1994). Under adverse conditions (e.g., drying out of the immediate environment or low temperatures), a plasmodium may convert into a hardened, resistant structure called a sclerotium, which is capable of reforming the plasmodium upon the return of favorable conditions. Moreover, amoeboflagellate cells can undergo a reversible transformation to dormant structures called microcysts. Both sclerotia and microcysts can remain viable for long periods of time and are probably very important in the continued survival of myxomycetes in some ecological situations and/or habitats.

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The presence of an assemblage of vascular and nonvascular epiphytes on the branches and to some extent the trunks of trees contributes to the development of a layer of accumulated organic matter derived from decaying epiphytes, partially decomposed tree bark, insect frass and intercepted litter. This microhabitat, which has been referred to as "canopy soil" (Stephenson & Landolt 2011) is known to represent an ecologically important subsystem of the forests in which it occurs but remains understudied for most groups of microorganisms (Orlovich et al. 2013). In an earlier paper, Stephenson & Landolt (2011) reviewed all records of which they were aware relating to the occurrence of dictyostelids (or cellular slime molds) in the canopy soil microhabitat. They reported that at least 37 species of dictyostelids had been recovered from more than 400 samples collected in 11 different localities throughout the world since the presence of these organisms in this microhabitat was first noted (Stephenson & Landolt 1998).

Myxomycetes are known to be common in ground soil (e.g., Stephenson et al. 2011), but there appear to be no previous reports in the literature relating specifically to their occurrence in canopy soil. However, an examination of records compiled when many of the samples mentioned above were processed for dictyostelids indicated that sets of samples collected in three localities (Monteverde [1998 and 2000], Cahuita [1997 and 2001] and Guanacaste [1998]) in Costa Rica, two localities in Northern Queensland, Australia (2002 and 2003) and one locality each in Honduras (2008), Puerto Rico (1995), Belize (2010), Ecuador (1998), the western United States (Oregon in 1998) and the eastern United States (Great Smoky Mountains National Park in 2000) yielded evidence of myxomycete plasmodia. The Oregon locality is a temperate coastal rain forest and the Great Smoky Mountains locality is a mid-latitude temperate forest, while all of the other localities are tropical forests, ranging from lowland tropical seasonal forests to lowland tropical rain forests to cloud forests. In some instances, only the fact that myxomycete plasmodia were observed in one or more cultures was noted, and no quantitative data were recorded. In other instances, data were collected for the proportion of samples yielding plasmodia, which ranged from 6% to 80%. In six of the sets of samples listed above, half or more produced plasmodia.

The occurrence of myxomycetes in the canopy soil microhabitat would not seem particularly surprising, since their amoeboflagellate cells presumably occupy a niche similar to that of the amoeboid cells of dictyostelids. Moreover, myxomycetes are often exceedingly common in the aerial litter microhabitat of tropical forests (e.g., Black et al. 2004) and their wind-dispersed spores seemingly would have no problem reaching above-ground microhabitats, whereas this is not the case for the spores of dictyostelids, which appear to have a limited potential for dispersal (Stephenson & Landolt 2011) and may depend largely upon animal vectors to reach such microhabitats.

The objective of this paper is to report these data and also more recent data obtained from a small set of samples of canopy soil collected from a temperate rain forest in southwestern New Zealand. The rain forest in question (located in the South West New Zealand World Heritage Area southwest of the town of Haast on the South Island, New Zealand) is the same forest described by Orlovich et al. (2013) in their study of ectomycorrhizal fungi in canopy soil. Unlike all of the samples examined previously, these recent samples were collected specifically in an effort to demonstrate the presence of myxomycetes. Seven samples were collected at an average height of approximately 11 m above the ground, with three samples collected from canopy soil that had developed on the branches of three different individual trees of the podocarp *Dacrycarpus dacrydoides* (A. Rich.) de Laub. and four samples from canopy soil that had developed on branches of four individual trees of the southern beech *Lophozonia menziesii* (Hook. f.) Heenan & Smissen. All samples were placed in small plastic bags and sent to the laboratory of the first author for processing.

In the laboratory, these samples were processed in essentially the same manner described by Stephenson & Landolt (2011) in their previous studies of the dictyostelids associated with canopy soil. Because several of the samples consisted of limited material, they were combined so that the actual number processed was only five (two from *Dacrycarpus dacrydoides* and three from *Lophozonia menziesii*). In brief, the laboratory procedures used followed the "Cavender method"

first outlined by Cavender & Raper (1965) and since used in numerous studies of dictyostelids. This involved determining the weight of each sample of canopy soil (or 5.0 grams if the weight exceeded this value) and then adding enough sterile distilled water to obtain a suspension of approximately 1:10. This mixture was shaken a number of times over a period of several minutes to disperse the material as thoroughly as possible. Afterwards, aliquots (each 0.5 ml) of the suspension obtained from a particular sample were added to each of three 100 by 15 ml disposal plastic Petri dishes containing hay infusion agar (Raper 1984). Approximately 0.4 ml of a heavy suspension of *E. coli* was added to each Petri dish, and the latter incubated under diffuse light at 22-25 C. Each inoculated plate was examined each day over a period of two weeks. Myxomycete plasmodia usually require a longer period of time than is the case for dictyostelids, so it is necessary to maintain plates for at least this long.

Three of the 15 plates (two plates prepared with one of the samples from *Lophozonia menziesii* and one plate prepared with a sample from *Dacrycarpus dacrydoides*) yielded the plasmodia of myxomycetes, with each positive plate producing several plasmodia (3, 4 and 6 plasmodia, respectively). Efforts to induce the formation of fruiting bodies were largely unsuccessful, even when plasmodia were transferred to types of media known to be suitable for culturing myxomycetes (Haskins & Wrigley de Basanta 2008). Fruiting bodies (identified as those of *Didymium squamulosum* [Alb. & Schwein.] Fr.) were obtained in only a single instance. Results from previous studies (Stephenson & Landolt 1996, Stephenson et al. 2004) have shown that plasmodia obtained in cultures of ground soil rarely form fruiting bodies. Just why this is the case is still unknown. The fact that a species of *Didymium* was recovered from canopy soil in the present study was not unexpected, since this appears to be dominant genus represented among the myxomycetes found in ground soil (Stephenson et al. 2011).

The relatively low percentage (3 of 15 total plates or 20%) of positive plates in the present study suggests that the frequency of occurrence of myxomycetes in canopy soil at this locality is not especially high, but the numbers of plasmodia recorded from those plates which were positive also suggests that in a particular microsite these organisms can be relatively common. Based on extensive field collecting throughout New Zealand by the first author (Stephenson 2003), myxomycetes do not seem to be very common in the moist temperate forests of southern New Zealand. Interestingly, the same situation appears to be true for the two other groups of "slime molds" found in terrestrial ecosystems—the dictyostelids (Cavender et al. 2002) and the protosteloid amoebae (Zahn et al. 2014). It is possible that the apparent low level of abundance of myxomycetes in the canopy soil of these forests simply reflects a similar response to some type limiting factor of the environment, although the lack of comparative data from other forest types, both in New Zealand and elsewhere, makes such a conclusion tentative a best. Although the data presented herein clearly document the occurrence of myxomycetes in canopy soil, they also indicate the need for additional investigations of this still understudied microhabitat.

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