ISSN 2215-650X
Slime Molds
Slime Molds **3** (2023) V3A5 https://doi.org/10.5281/zenodo.6998855

The importance of substrate properties in the occurrence of species of myxomycetes

Peter Wellman[1]

[1]17 Warragamba Avenue, Duffy, ACT, 2611 Australia

E-mail: wellmanp@iinet.net.au

Received: 23 May 2022
Accepted for publication: 16 August 2022
Published: 17 August 2022
Corresponding editor: Steven L. Stephenson

Abstract: This paper investigated the effects that the physical and chemical properties of a particular substrate have in determining the relative importance of common and uncommon species of myxomycete. The paper used bark collected within four substrate types (generally a tree genus). Within each substrate type the physical and chemical properties are assumed to be very similar. Many samples of several of these substrate types were cultivated using the moist chamber culture method with a hypothesized condition of high competition. For samples within a substrate type, over a continental size area, results showed that the same eight common species recurrently occurred. These eight common species generated 66% of all records. The probability of one of these common species occurring in one sample with mixed material in five Petri dishes is 60-80%. This study supports the view that the occurrence of a particular species of myxomycete is strongly controlled by substrate properties. This strong control is hypothesized to be unlikely if cultivation is carried out with low competition.

Keywords: slime molds, substrate control, species associations

Introduction

In myxomycete research a lot of effort has gone into describing the different species of myxomycetes, documenting where these species have been found and investigating their ecology (Takahashi 2015; Schnittler et al. 2016; Stephenson et al. 2020). Recently, a numeric model has been derived for calculating a myxomycete species' preferred substrate (Wellman 2021, unpublished). The present paper estimated the effect of a myxomycete species' preferred substrate properties in determining the relative importance of common and uncommon species in a sample's species assemblage. In this manner, the exercise shown herein represents a check on the reality of the mentioned numeric model.

The myxomycete assemblage found on single tree-species substrate after a watering event is thought to vary due to (1) the chemical, physical and other properties of the substrate, (2) the magnitude and separation of watering events, (3) whether the normal myxomycete assemblage has existing resting phases, or whether they have been destroyed by an unusual event such as a fire (Adamonytė et al. 2016), (4) whether conditions for myxomycete species growth on the substrate encourage an equilibrium myxomycete species assemblage or encourage the growth of single species in isolation, and (5 the decay stage of the substrate (Takahashi 2004). If these factors are held reasonably constant, then we can look at features of the normal species association. This paper looks at whether, if we keep the known factors that influence species occurrence constant, results show the same small group of dominant species of myxomycetes for each sample of a substrate type (such as the bark of a tree genus). If this occurs over a continental size area, there would be strong support for substrate properties being a main control of the occurrence of particular species.

Materials and methods

The Australian data set (from Wellman 2019) used in the main part of this paper was collected to minimize external factors as follows. The substrate properties were thought to be maintained reasonably constant by using only data collected on substrates within a tree genus (or bark type for *Eucalyptus*) so the pH, density and amount of surface and internal water would only have small variations. The substrates were generally collected during winter, which has low mean rainfall over most of Australia, and after one to two months with no significant rain, so the time since the last rainfall event did not significantly affect the results. The growth of sporocarps of myxomycetes was encouraged by collecting small pieces of as wide a range of the bark substrates as possible and putting a range of fragments of these pieces in each Petri dish for cultivation by using the moist culture method. This was thought to ensure that species efficient on that substrate would dominate the microcosm and that the occurrence of rare species would be minimised. Five Petri dishes were cultivated per sample so the collected crop from each sample was reasonably large. The substrate used was dead bark on a living tree as this would give the largest myxomycete crop. Old trees were used because their bark has a range of decay, thus minimising the effect of the state of decay of the substrate.

The Australian data set used in this paper was composed of samples collected over much of Australia but omitted the relatively small coastal area with higher rainfall that originally had closed forests. The areas sampled ranged from tropical open woodland, through various arid and semi-arid areas (woodland with grass to grass/scrubland with a few trees) to temperate woodland. The annual rainfall of these areas normally ranges from 200 to 1500 mm. Samples were collected on very long traverses across Australia along main roads. One or more samples were collected at stops approximately 50 to 100 km apart. The dataset comprised about 350 samples and 2000 records. Where below I refer to the species of a sample, I am referring to the species found in all five Petri dishes.

When a substrate sample is cultivated using the moist chamber culture method, the composition of the species association obtained depends in part on the strength of interspecific competition within the Petri dishes. A substrate sample for moist culture would consist of one or many substrate pieces. If the aim of the cultivation is to determine which species of myxomycete, however rare, have resting phases within the substrate, then it could be relevant to minimise myxomycete competition in each Petri dish. I hypothesized that this could done by putting fragments of only one or a few pieces in each Petri dish. There will be fewer species feeding, less competition and species that have substrate preferences dissimilar to the substrate can better survive. If the aim of the cultivation is to determine the species in resting phases that have similar substrate preferences for the substrate, then the maximization of myxomycete competition in each Petri dish could be necessary. I hypothesized that this could be done by putting fragments of as many pieces as possible in each Petri dish. High and low competition both result in fruiting bodies of only those species that are present in the sample as resting phases, so both methods are valid, but the resulting species assemblages would differ. Low competition culture is presumed to give fewer common species and more uncommon species, and high competition culture is thought to yield more common species and fewer uncommon species. The duration of the sample growth event with low competition is longer than 40 days (Schnittler 2001), and with high competition is less than 28 days (Wellman 2019).

Results

The dominance of the very common species

What is discussed below are the myxomycete species associations for samples grown in the Australian survey on the four most common Australian tree bark groups. The dominance effect is subject to random variation, so I used the largest homogenous groups that were possible. These four bark groups were those of the following tree genera: *Acacia* (symbol Ac; 67 samples, 47 species and 346 records), *Corymbia* (Cor; 25 samples, 27 species and 93 records), *Callitris* and *Casuarina* (Cal+Cas; 31 samples, 46 species and 179 records), and the *Eucalyptus* with 'box' and 'coolabah' type barks (Eb+Ec; 55 samples, 55 species and 307 records). The data on species occurrences is given in Table 1. The table for each bark type can be divided into two sections, and the upper part with accumulated volume 0-33% gives the species with few records. In this group there are numerous species and they make up only 33% of the total records. The lower part of the table has accumulated volumes 33-100%. In this group there are few species (8-13), and in total these species make up 66% of the total records. Some 66% of the records for *Acacia* are provided by 8 of the 47 recorded species, for *Corymbia* it is 8 of the 27 species, for *Cal+Cas* it is 8 of the 46 species, and for *Eb+Ecs* it is 13 of 55 species. Both *Cal+Cas and Eb+Ecs* are composite groups so would have a greater scatter in properties than a single tree genus. Hence this data is consistent with the properties of a tree genus bark substrate controlling myxomycete species occurrence such that generally the eight common myxomycete species of a substrate type give 66% of the records for samples over a continent.

This conclusion may be suprising to people only used to cultivation of myxomycetes using conditions of low competition (as considered herein). However, there are two considerations. These records of common species would not be obtained if the resting phases were not in the samples. Cultivation with strong competition seems to encourage species that efficiently produce sporocarps on that substrate.

The reliability of the conclusion of eight common species on a substrate giving 66% of the records is difficult to quantify. The data is based on 178 samples and 900 Petri dishes. This is a reasonably sized myxomycete moist chamber culture survey. When the 178 samples were broken into four groups, then each of these groups showed the same result. The 178 samples used had sites spread over the Australian landmass of 4000 x 2000 km size, collected over a period of six years, and the samples included multiple species within each tree genus. So the sample collection is random. A survey based on a larger number of samples, fewer than five Petri dishes per sample, and the same number of Petri dishes may come to a more reliable conclusion, but this increased reliability would refer to the common species having a percentage of the records smaller than 66%.

Table 1. The dominance of the most common species in a sample species assemblage. This table gives data for four substrate types. For tree abbreviations see Materials and Methods.

	Ac			**Eb+Ec**			**Cal+Cas**			**Cor**	
Number of records	**Number of species**	**Percentage of accumulated species**	**Number of records**	**Number of species**	**Percentage of accumulated species**	**Number of records**	**Number of species**	**Percentage of accumulated species**	**Number of records**	**Number of species**	**Percentage of accumulated species**
1	18	0	1	22	7	1	16	1	1	13	14
2	6	2	2	7	12	2	8	3	2	3	20
3	6	3	3	4	16	3	4	8	3	1	24
4	3	6	4	2	18	4	3	14	4	3	37
5	1	10	5	1	20	5	4	22	5	1	42
6	1	14	6	4	28	6	3	32	6	1	48
8	1	19	8	2	33	8	3	45	7	3	71
14	1	26	9	1	36	9	2	61	8	1	80
19	2	33	10	3	46	11	1	79	19	1	100
21	1	41	11	1	49	13	2	100			
22	3	51	12	2	57						
26	1	61	16	2	68						
28	1	73	21	1	75						
33	1	86	22	1	82						
36	1	100	27	1	91						
			29	1	100						

Occurrence rate of common species

The most widespread tree genus in Australia is *Acacia* (wattle). Trees sampled have old bark with deep, vertical slits around the trunk. There were 59 samples. The number of myxomycete records per sample ranged from 1 to 11. If we take the 28 samples for which the records per sample range from 6 to 11, then 11 species are common. They have between 8 and 23 records. Table 2 lists the species that are common, and the number of records per species. These give a raw average probability of occurrence (species/record) of 53%. However the average number of records in a sample was 7, and there were 11 common species so they cannot all occur. The corrected average probability of occurrence is 53% x 11/7 = 83%. Table 2 shows that when this calculation is repeated with a subset of the samples with only 8 to 11 records then we get a similar result of 77%.

Table 2. Number of records of myxomycetes, indicators of survey performance and corresponding species documented on *Acacia* bark arranged by sampling effort.

Species and indicators	**Sampling effort**	
	28 samples	**14 samples**
Badhamiopsis ainoae	17	9
Calomyxa metallica	10	9
Comatricha ellae	15	9
Didymium dubium	15	9
Licea biforis	13	7
Licea kleistobolus	22	12
Licea operculata	11	7
Licea scyphoides	9	6
Macbrideola oblonga	13	7
Physarum decipiens	22	12
Physarum leucophaeum	12	8
Number of records in samples	6-11	8-11
Average number of records	14.4	8.6
Average probability of occurrence	53%	62%
Corrected percent average	83%	77%

These calculations show that the bark properties of *Acacia* throughout Australia are sufficiently constant that they provide a strong constraint on the associated myxomycete species association. The species association is constant even though average annual rainfall varies from 200 to 1000 mm per year. Each common species would on average have an 80% chance of occurring in each sample if the sample has enough records. However, this result for *Acacia* is unusual in that the tree has been sampled primarily in arid Australia. Of the common myxomycete species, the four species (*Badhamiopsis ainoae, Didymium dubium, Macbrideola oblonga* and *Physarum decipiens*) mainly occur in arid areas, both in Australia and overseas. If we consider *Eucalyptus* bark samples (Eb/Ec) with over seven records per sample, there are 19 samples, 176 records and 45 myxomycete species. The seven most common myxomycete species found (*Physarum decipiens, Licea kleistobolus, Acyria cinerea, Perichaena vermicularis, Cribraria violacea, Didymium dubium,* and *Physarum leucophaeum*) have an average of 12 records, so these seven species have a probability of occurrence of 12/19, or 63%. Only two of these species occur mainly in arid areas. This Eb/Ec group consists of two bark types with different, but similar properties, so the 63% is a minimum estimate.

Another informative set of data is that from *Pinus* (pine tree) samples from around the world; Lithuania, Arkansas and Tennessee in USA, India, Australia and Costa Rica. Data from Alaska (Schnittler et al 2016) were not used as the species of myxomycetes found reflect the Arctic climate. Table 3 shows the data. Adamonytė et al. (2016) and Stephenson et al. (2020) fully reported the species found, while Snell and Keller (2003) reported only the common species.

Table 3. Species of myxomycete on *Pinus* bark as reported in several previous studies.

Country	**Lith**[a]	**Lith**[a]	**USA**[b] **Ark**	**USA**[c] **Ten***	**India**[b]	**Aust**[b]	**CR**[b]
***Pinus* symbol**	**Pm**	**Ps**	**SP**		**ChP**	**MP**	**CaP**
Latitude	**56ºN**	**56ºN**	**36ºN**	**36ºN**	**31ºN**	**30ºS**	**10ºN**
Mean pH	**4.2**	**3.8**	**4.2**	**3.8**	**5.6**	**3.8**	**4.6**
Arcyria cinerea	12	35	3	14	4	1	3
Clasterderma debaryanum				10	10	4	4
Comatricha elegans			10			33	3
Cribraria confusa			6	12	6		24
Cribraria microcarpa		1					1
Cribraria minutissima			17		1	7	
Diderma effusum	4				1		
Diderma hemisphaericum			1		6		3
Echinostelium apitectum	64	42	6		2		
Echinostelium minutum	82	39	47	40	29	47	15
Enerthenema papillatum	5	22	12	30	1	5	
Licea kleistobolus	33	72	20	2	41		
Licea minima	6	3					
Licea operculata			7		2		8
Licea parasitica	96	7					
Licea pygmaea	5	1					
Paradia. fimbriata	2	32				14	
Paradia. solitaria	34	7	2			34	
Physarum album	1		4		4		9
Physarum galbeum			7				1
Physarum viride	28						11
Other records	2	3	4	4	4	1	6

[a]Adamonytė et al. 2016; [b]Stephenson et al. 2020; [c]Snell and Keller, 2003.
*Incomplete reporting

The two Lithuanian *Pinus* species of Adamonytė et al. (2016) were essentially from the same plantation. The two *Pinus* species had samples affected by fire and not affected by fire and the data used herein corresponded to the treatment of *Pinus* not affected by fire. The sites reported varied greatly in latitude, and are from a wide range of locations around the world. Between the sites there was no significant systematic difference in the species present so the data was consistent with belonging to one species association controlled by the *Pinus* bark substrate. It is difficult to numerically analyse all this data set because of the sampling and reporting differences between the three papers. We can obtain six independent, widely spaced surveys by rejecting one of the Lithuanian surveys. The result from Table 2 is that 13 myxomycete species are recorded in at least 3 of the 6 locations, giving 50 records. Hence, these 13 species have a greater than 50/(13x6) = 64% probability of occurrence in a survey with *Pinus* bark substrate. This estimate is a minimum because the Tennessee data is not fully reported. These Petri dishes were cultivated by unmixed substrate pieces to encourage uncommon species.

Hence the probability of occurrrence of a common myxomycete species in a sample is less than 80% for *Acacia*, greater than 63% for *Eucalyptus* of the 'box' or 'coolabah' type, and for species in a survey is greater than 64% for *Pinus*.

In conclusion, samples from a single substrate type, at well-spaced sites on a continent yield the same common myxomycete species in moist chamber cultures. For the four substrate types studied the eight myxomycete that were common on high competition cultivation gave 66% of the records. The apparent probability of occurrence of one of those common species on one sample was about 64–80%, but these values depend on survey design and the size of the survey. These observations are consistent with substrate properties being a major control on the myxomycete species occurrence.

Acknowledgements

I am very grateful for comments by the reviewers. I wish to thank the Australian National Herbarium for use of library facilities.

References

Adamonytė G, Moiejūnaitė J, Uršėnaitė R. 2016. Crown fire and surface fire: effects on myxomycetes inhabiting pine plantations. Sci Total Environ. 572: 1431-1439.

Schnittler M, Dagamac NHA, Sauke M, Wilmking M, Buras A, Ahlgrimm S, Eusemann P. 2016. Ecological factors limiting occurrence of corticolous myxomycetes – a case study from Alaska. Fungal Ecol. 21: 16-23.

Snell KL, Keller HW. 2003. Vertical distribution and assemblages of corticolous myxomycetes on five tree species in the Great Smoky Mountains National Park. Mycologia 95(4): 565-576.

Stephenson SL, Marbaniang TM, Gupta P, Rojas, C. 2020. Assemblages of corticolous myxomycetes associated with species of *Pinus* (Pinaceae) in four different regions of the world. Nova Hedwigia 111 (1-2): 199-217.

Takahashi K. 2004. Distribution of myxomycetes on different decay states of deciduous broadleaf and coniferous wood in a natural temperate forest in the southwest of Japan. Syst Geog Pl. 74: 133-142.

Takahashi K. 2015. Distribution of Myxomycetes on Varied Leaf Litter Types in a Mixed Forest in Warm-Temperate Western Japan. Open J For. 5(7): 60087.

Wellman P. 2019 Australian corticolous myxomycetes: models of distribution and development. Aust J Bot. 67: 617-629.

Wellman P. 2021 Controls on myxomycete species and species associations. Aust J Bot. 69: 30-44.