Seasonality and sequential occurrence of fungi on wood submerged in Tai Po Kau Forest Stream, Hong Kong

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The effects of seasonality on freshwater lignicolous fungi in Tai Po Kau Forest Stream was investigated by examining the fungal communities on naturally occurring submerged wood. Fungal succession (sequential occurrence of sporulating fungi) was also investigated by studying changes of fungal communities on wood baits of Machilus velutina and Pinus massoniana over 21 months. Higher species richness, fewer dominant fungi and more infrequent fungi were found on naturally occurring submerged wood during the hot wet season, as compared to the cool dry season. Fungal communities were variable on collections made over different hot wet seasons, but the communities were consistent during the cool dry season Aniptodera chesapeakensis, Massarina ingoldiana and Sporoschisma collections. nigroseptatum dominated the fungal communities during the cool dry season, while Nectria cf. byssicola was dominant during the hot wet season. During 21 months submersion of wood baits of Machilus velutina and Pinus massoniana, three distinct types of fungal communities were observed, i.e. pioneer, early and later successional groups. Higher species richness and more dominant fungi were found on both wood types during the early successional stage. Differences in successional groups were more prominent on wood baits of *Pinus massoniana*. Fungal communities on wood baits of Machilus velutina and Pinus massoniana were similar during both pioneer and early successional stages, but differed at the later successional stage. Nectria cf. byssicola, Sporoschisma nigroseptatum and S. uniseptatum were early colonisers on both wood types. Savoryella lignicola was a later coloniser on Machilus velutina, while Dictyosporium digitatum, Massarina bipolaris and M. ingoldiana were later colonisers on Pinus massoniana. A total of 175 fungi, including 56 ascomycetes, 1 basidiomycete, 115 anamorphic fungi, 2 myxomycetes and 1 zygomycete, were recorded in this study.

Key words: freshwater lignicolous fungi, fungal ecology, wood decomposition.

Introduction

Seasonal occurrence and succession of fungi on leaves submerged in streams in tropical and temperate regions are well studied (Bärlocher, 1992a). Higher species richness has been recorded after leaf fall and / or following the

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start of the wet season. Prominent succession patterns of individual fungi, or groups of fungi, on leaf substrata were not observed, primarily due to the short time it takes for the leaves to decay (Bärlocher, 1992a). There has only been one study that has investigated seasonal occurrence of freshwater fungi on wood (Lamore and Goos, 1978). Seven studies have investigated the succession of freshwater fungi on woody substrata in temperate regions (Willoughby and Archer, 1973; Sanders and Anderson, 1979; Shearer and von Bodman, 1983; Roldán *et al.*, 1989; Révay and Gönczöl, 1990; Shearer and Webster, 1991; Gönczöl and Révay, 1993), while only one such study has been conducted in the tropics (Sivichai *et al.*, 2000).

This present study was undertaken in a subtropical stream to investigate (1) the diversity of fungi on naturally occurring submerged wood samples; (2) the diversity of fungi on baits of two different wood types; (3) if hot wet and cool dry seasons influence the fungal communities on submerged decaying wood; (4) if fungal succession occurs on the two wood types; and (5) if different fungal communities are found on different wood types. The experiment on succession was run in parallel to that on seasonality in order to determine if any temporal variation in species composition was due to fungal succession or to fungal seasonality. The present study is compared with other seasonal and succession studies.

Methods

Study site

Tai Po Kau Special Area (22°27'N 114°11'E) is the earliest established natural reserved area in Hong Kong, covering 460 hectares and composed of secondary forest, with more than 100 tree species, mostly native to South China (Government of Hong Kong, 1982; Nicholson, 1994). The area is known locally as Tsung Tsai Yuen, meaning "Pine Garden", due to the dominance of *Pinus massoniana* (Chinese Pine). *Machilus velutina* is also commonly found within the reserve. The main drainage of the reserve area, Tai Po Kau Forest Stream, is 3.6 km long, arising 400 m above sea level. The general features and hydrology of the stream have been reported by Dudgeon (1982, 1992).

The climate in Hong Kong is subtropical, tending towards temperate for nearly half of the year. There are two seasons in Hong Kong: wet and hot season due to the prevalent south-western monsoon (April to September), and dry and cool season due to the prevalent north-eastern monsoon (October to the following March). The climate in 1996 was typical, but the climate in 1997 was unusual with high rainfall. The high rainfall recorded in September 1996

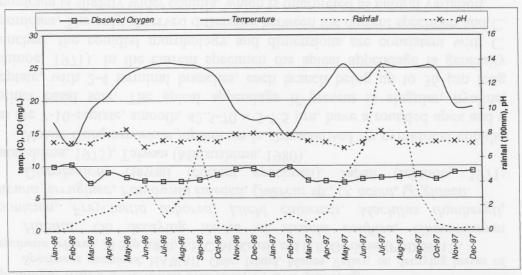


Fig. 1. Monthly rainfall, water temperature, dissolved oxygen and pH values of Tai Po Kau Forest Stream in 1996 and 1997 (Government of the Hong Kong SAR).

was due to the Typhoons Sally and Willie. The rainfall in 1997 was the highest since records began in 1884, with double the normal rainfall recorded during June to August. The abnormally higher rainfall recorded in August (Fig. 1) was primarily due to the Typhoons Victor and Zita (Government of the Hong Kong SAR, 1998). The water temperature ranged from 13.1 / 14.5 C (February 1996 / 1997) to 25.8 / 25.4 C (July 1996 / 1997) (Fig. 1). The stream water was near neutral with a pH of 6.77 to 8.3, and the dissolved oxygen was high at 7.34 to 10.22 mg/L (Fig. 1).

Experimental design

Fifty samples of naturally occurring submerged decaying wood were randomly collected from Tai Po Kau Forest Stream during the hot wet (June and September) and cool dry seasons (March and December) in 1996 and 1997, to examine whether these seasons influence the fungal communities on submerged decaying wood. In order to test whether different fungal communities are found during different stages of wood decay, wood baits were introduced into Tai Po Kau Forest Stream. In order to examine simultaneously whether different wood types affect the colonisation of fungal communities, two types of wood baits, *Machilus velutina* and *Pinus massoniana*, were used.

Branches of living trees of *Machilus velutina* and *Pinus massoniana* were cut to $20 \times 1.5 \times 1.5$ cm size and air dried for two months. Non-sterilized wood baits were used because Révay and Gönczöl (1990) concluded that no significant differences were obtained between fungi found on sterile and non-

sterile wood baits submerged in a stream. In order to examine what fungi were present and able to sporulate on the air-dried wood used in this experiment before submersion in the stream, a pre-trial was conducted. Thirty air-dried wood samples were incubated in sterile moist chambers. A second set of 30 air-dried wood samples were incubated in sterile moist chambers following submersion in an aeration chamber.

Wood baits were drilled with a hole at each end. A set of 40 baits was strung through the holes (20 pieces of each wood type, alternately) between 2 nylon ropes, so that it resembled a ladder. In previous successional studies of fungi in freshwater habitats, baits were grouped together, either in packs or within bags. This facilitates colonisation of fungi within groups (Maltby, 1996), but thus potentially imposes inadequacy in experimental design since all replicates should be independent of each other. To minimize the grouping effect, all baits in this study were tied in parallel, 2 cm apart. The resulting chains of baits were stretched out on the stream bottom with at least one stone attached at each end to prevent overlaying of the baits and to avoid being washed away by floods. A total of 7 sample sets were introduced into Tai Po Kau Forest Stream on March 1996. One set of samples was retrieved every 3 months on the same dates as the collection of naturally occurring submerged wood.

All samples collected were incubated in damp chambers and examined under a light microscope periodically within 1 week to 1 month.

Data analysis

Fungi found in this study are presented in terms of relative abundance, that is the mean percentage of community belonging to the species (Yanna et al., 2002). Fungi with relative abundance $\geq 10\%$ are regarded as dominant species. These fungi are plotted to illustrate changes in the dominant species through the experimental period. Differences in the fungal communities from various collections were compared by 3-dimensional correspondence analysis (Booth and Kenkel, 1986; Anonymous, 1995). All the analyses were carried out on fungi forming fruiting bodies on the sample surface.

Results

A total of 175 fungi, including 56 ascomycetes, 1 basidiomycete, 115 anamorphic fungi, 2 myxomycetes and 1 zygomycete, were recorded in this study (Table 1). One hundred and fifty-five fungi were recorded on naturally occurring submerged wood, while 58 fungi were recorded on baits of *Machilus velutina* and also 58 on *Pinus massoniana* (Table 1). The numbers of fungi on each sample were stable on naturally occurring submerged wood (2.5-3.8), but

Table 1. Percentage abundance of fungi found on different wood types submerged in Tai Po Kau Forest Stream.

Species	Nat	turall	y occ	curri	ng w	ood		Ma	chilu.	s veli	ıtina				Pin	us m	assor	iiana			
Distrocted analysis							N-7	M-1	M-2	M-3	M-4	M-5	M-6	M-7				P-4		P-6	P-7
Ascomycetes			18	19	2				9			15		33							
Aniptodera chesapeakensis	5	2	8	10	6	8	17	4	7	24	1	14	17	20	2	22	10	19	3		
Aniptodera lignatilis	1	1	1							2											
Annulatascus aquaticus	1																				
Annulatascus crassitunicatus	1		1				1							2							
Annulatascus incrustatus		1				1	1														
Annulatascus triseptatus	1	1	2		1		1														
Annulatascus velatisporus	2	1			1	1															
Apiosordaria hongkongensis		1																			
Aquaticola ellipsoidea	6	1	4	4	5	8	10	4	3	6	5	7	11	4	6	13	13	7	8		
Aquaticola hyalomura	2	1	3	1	2		2														
Aquaticola sp.	2	3	1	1	3	5													1		
Arnium apiculatum	1																				
Ascolacicola aquatica					1																
Boerlagiomyces lacunosispora									2								1				
Cataractispora appendiculata						1							3								
Cataractispora viscosa	1				1		1														
Cercophora appalachianensis	1	1	1			1			6				13							14	
Cercophora coprophila	1		1	1	2							7		2	2				2		
Ceriospora hongkongensis					1	1													_		
Chaetosphaeria anglica					1																
Chaetosphaeria lentomita	1	1			2		1														
Diaporthe beckhausii		1				1															
Erostella minutissima		1																			
Gnomoniella rubicola	1		1		1	1	1														
Halosarpheia heteroguttulata								2													
Hymenoscyphus sp.			1																		
Hypoxylon kretzschmarioides				1																	

Table 1 continued.

Species	Nat	urall	y occ	curri	ng w	ood		Mad	chilus	veli	utina						assor				
	N-1	N-2	N-3	N-4	N-5	N-6	N-7	M-1	M-2	M-3	M-4	M-5	M-6	M-7	P-1	P-2	P-3	P-4	P-5	P-6	P-7
Jahnula aquatica				1														1			
Jahnula australiensis		1				1															
Jahnula bipolaris				1		2	3					1				2		2			
Jahnula systyla																1					
Lasiosphaeria sp.	1	1			1	1															
Massarina bipolaris	1	2	1	1		1	1		1		10						1		7	16	23
Massarina ingoldiana	1	1	4	5	1	2	3		12		11	1					1		12	29	25
Massarina lignicola			1																		
Massarina thalassioidea		3	1	1	1		2														
Microthyrium sp.												3									
Nectria cf. byssicola	1	3	1	1	1	2		13							22	3					
Nectria pallidula					1																
Neolinocarpon inconspicuus		1																			
Ophioceras dolichostomum		1	1																		
Orbilia luteorubella			1	1	1	1															
Ornatispora hongkongensis	1																				
Phomatospora berkeleyi					1	2															
Potamomyces aquatica		1																			
Pseudohalonectria adversaria	1			1	1							1		2							
Pseudohalonectria lignicola	1	1	1	1	1	1															
Rhamphoria pyriformis	1	1			1																
Savoryella aquatica			1										2								
Savoryella fusiformis				1					1							1					
Savoryella lignicola	5	2	10	14	5	11	10		8	13	5	15	23	29		1	7	8	11	2	
Sordaria humana			1																		
Strossmayeria curvatis					1																
Tamsiniella labiosa			1	2	1	2	4		1		5						1	2	1		
Torrentispora fibrosa	1	1	1		5	2															

Table 1 continued.

Species	Nat	urall	y occ	curri	ng w	ood		Me	ichil	us ve	lutine	7			Pin	us m	assor	iiana	ı		
•		N-2					N-7	M-	1 M-	2 M-	3 M-	4 M-	5 M-	6 M-	7 P-1	P-2	P-3	P-4	P-5	P-6	P-7
Basidiomycete						×															
Acanthophyses-like structures		1	1		1																
Anamorphic fungi																					
Acrogenospora sphaerocephala	1	2		1	1	1									2				1		
Anamorphic fungus sp. 2		1																			
Anungitea heterospora			1	1																	
Badarisama minuta		1																			
Berkleasmium corticola		1																			
Berkleasmium moriforme	1		1		1	2										2		2	1		
Brachiosphaeria tropicalis																		1			
Brachydesmiella caudata		1		1					. 2			1	2						2		
Brachysporiella gayana	1	1			1																
Camposporium antennatum					1				2			5	2	4					2		
Canalisporium caribense		1				1															
Canalisporium pallidum			1																		
Candelabrum brocchiatum	9	3	4	9	11	5	2		2	2		5	5	2		2		1		2	
Ceuthospora gaeumannii											2										
Chaetopsina hongkongensis		1						2	1							1		1			2
Chaetospermum camelliae								2										7			_
Cheiromyces lignicola			1	1				_			1								1		
Chloridium sp.	1		î								S								•		
Chloridium lignicola	1																				
Chloridium sp.	1		1	1	1																
Chloridium pachytrachelum	•	1	-	-	•																
Chloridium virescens var. caudigerum	2	•			1																

Table 1 continued.

Species	Nat	ural	y oc	curri	ng w	ood		Ma	chilu	is vel	utina	ı			Pin	us m	assor	iiana	!		
							N-7	M-1	1 M-2	2 M-3	3 M-4	4 M-	5 M-6	M-7	P-1	P-2	P-3	P-4	P-5	P-6	P-7
Chloridium virescens var. virescens			1		1		1														2
Cirrenalia macrocephala		1	1																		
Clohesyomyces aquaticus			1																		
Coleodictyospora micronesica					1																
Cordana abramovii var. seychellensis	1																				
Cordana musae		1																			
Cryptophiale iriomoteanum	- 1																				
Cylindrocarpon olidum					1					10											
Cylindrocladium parvum					1						1	1					1				
Dactylaria irregularis		1	1	2						2	2							2	1		
Dactylaria lakebarrinensis			1	1																	
Dactylaria triseptata					1								2								
Dictyochaeta fertilis		1								3		1					1	1	1		
Dictyosporium alatum			1									1			6						
Dictyosporium atroapicis			1			1			2												
Dictyosporium digitatum		1	2				2		8		10	3				1	3	1	7	16	15
Dictyosporium elegans		1		1	1	2	2	13	11		14	1			4	1	10		9	12	8
Dictyosporium micronesicum	1						1				2	1									
Dictyosporium toruloides																	1				
Didymostilbe australiensis				1																	
Didymostilbe oblongata		1																			
Diplocladiella scalaroides										3											
Ellisembia opaca	1	1	1		3	2															
Endophragmia inaequiseptata		1																			
Endophragmiella mexicana				1																	
Endophragmiella occidentalis	1																				

Table 1 continued.

Species	Nat	tural	ly occ	curri	ng w	ood		Ma	chili	is vel	lutina	t			Pin	us m	asson	iiana	!		
·							N-7	M-	1 M-	2 M-	3 M-4	M-	5 M-6	6 M-7	P-1	P-2	P-3	P-4	P-5	P-6	P-7
Endophragmiella ramificata		1																			
Exserticlava triseptata		1	1																		
Exserticlava vasiformis	1	2	3		1	3	2				2										
Gliocladium cylindrosporum		1		1														1			
Gliocladium solani								4	4		1					1					
Gonytrichum chlamydosporium var. simile		1			1																
Haplochalara angulospora		1																			
Helicoma sympodiophorum	1																				
Helicomyces roseus		3	3	2	2	1	2		2		5	3		4		7	3	4	1		2
Helicomyces torquatus										2					2						
Helicosporium guianensis					1																
Helicosporium lumbricoides	2		2	6								3						3			
Janetia curviapicis		1				1															
Kameshwaromyces globosus	3	3	3	2	5	2	3		1			7	2	8		3		4	2		
Kylindra trisepata				1																	
Lauriomyces pulcher			2		1																
Listeromyces insignis		1			1																
Margaritispora hongkongensis																			1		
Melanocephala australiensis	3	1	1		1	1	2	2		2						2		1			
Melanocephala triseptata	1																				
Monodictys abuensis		1			1	1	1									7					
Monodictys capensis					1																
Monodictys gemmipara	1																				
Monodictys pandani	1																	1			
Monodictys peruviana		1																			
Monodictys sp.		1	1		1																
Monotosporella rhizoidea					1																

Table 1 continued.

Species	Nat	urall	у осс	curri	ng w	ood		Ma	chili	ıs vel	utina	ı			Pin	us m	assor	iiana	!		
	N-1	N-2	N-3	N-4	N-5	N-6	N-7	М-	1 M-	2 M-3	3 M-4	1 M-	5 M-6	M-7	P-1	P-2	P-3	P-4	P-5	P-6	P-7
Monotosporella setosa var. macrospora	4	3	3	1	2	3	2														
Nawawia filiformis	1		1	1	1	2															
Paecilomyces laeensis				1																	
Paecilomyces marquandii					1			2	1												
Papulasporella appendiculata									2												
Peyronelina glomerulata			1	3								3	6	4		4		5	1		
Phaeoisaria clematidis	1	1	2	1	3	1	1														
Phialocephala xalapensis	1	1					1								2						
Phoma cf. complanata		1																			
Pleurothecium recurvatum	1		1			1															
Pseudospiropes cubensis	1																				
Ramichloridium fasciculatum			1			1															
Sagenomella verticillata	1									2											
Sibirina orthospora		1														1					
Spadicoides atra		1																			
Spadicoides klotzschii																	1				
Spadicoides obovata																	1		1		
Speiropsis scopiformis																		1			
Spirosphaera floriformis			1	6	1		3	2	6	14	11	4	3	10		4	21	5	10	8	19
Sporidesmiella hyalosperma var.	1	1			1																
hyalosperma																					
Sporidesmium bambusicola		1																			
Sporidesmium filiferum			1		2																
Sporoschisma nigroseptatum	4	3	7	6	4	6	10	29	15	11	12	4			22	8	17	3	10	2	6
Sporoschisma saccardoi	1	1			2	1		2				100			2	-	3	1		_	-
Sporoschisma uniseptatum	6	3	4	6	1	8	5	4	2	2	2	1			15	9		6	1		
Stachybotrys queenslandica																			1		

Table 1 continued.

Species	Nat	tural	ly oc	curri	ng w	rood		Ma	chili	is vel	utina	ı			Pin	us m	asso	nian	a		
			N-3				N-7	M-	1 M-2	2 M-3	3 M-4	4 M-	5 M-0	6 M-	7 P-1	P-2	P-3	P-4	P-5	P-6	P-'
Staurospora hongkongensis			1																		
Stilbella holubovae						1		2			2	3		2	11	2		6			
Sympodicum hongkongensis	1	1	2																		
Trichoderma piluliferum				1														1			
Trichoderma polysporum		1			1																
Tricladium indicum		1		2			2			2				4			1		1		
Uberispora heteroseptata							1														
Uberispora hongkongensis		1																			
Umbelopsis versiformis										2											
Veronaea botryosa				1																	
Verticillium sp. 1	1	3	3	2	1		3	7	1						4			3			
Verticillium sp. 2		3	2		1																
Wiesneriomyces javanicus																		1			
Xylomyces chlamydosporis	2	1	1			6	1					7	11	4		1		9	1		
Myxomycetes																					
Cribraria violacea	2			1																	
Dictydium cancellatum	1	1																			
Zygomycete																					
Montierella sp.								2		2											
No. of species per sample	2.9	2.9	3.8	3.6	3.7	2.6	2.5	2.3	6.2	3.2	6.2	6.1	3.3	2.6	2.7	7.3	3.6	5.5	5.1	2.6	2.7
Species richness	62	79	64	47	67	45	35	17	25	18	20	26	14	15	14	24	19	30	28	9	9
Total species richness	155							58							58						

fluctuated between 2.3-6.2 on *Machilus velutina* and between 2.6-7.3 on *Pinus massoniana* (Table 1).

It was established from the pre-trial samples, that only *Pestalotiopsis* spp. and basidiomycete mycelial mats occurred on samples directly incubated in damp chambers without presubmersion in the stream, while basidiomycete mycelial mats were found on submerged samples aerated for one month and then incubated in moist chambers. These fungi were not recorded on wood submerged in streams.

Seasonal variations in fungal communities

Species richness on naturally occurring submerged wood increased during the hot wet season and decreased during the cool dry season (Table 1). A higher number of dominant fungi (relative abundance $\geq 10\%$) were found on wood collected during cool dry season (1-4 dominant fungi), as compared with those collected during the hot wet season (0-1 dominant fungus). The number of infrequent fungi (relative abundance = 1%) increased during wet season and declined during the dry season (number of infrequent fungi of N1-N7: 46, 63, 45, 31, 50, 24, 14; Fig. 2).

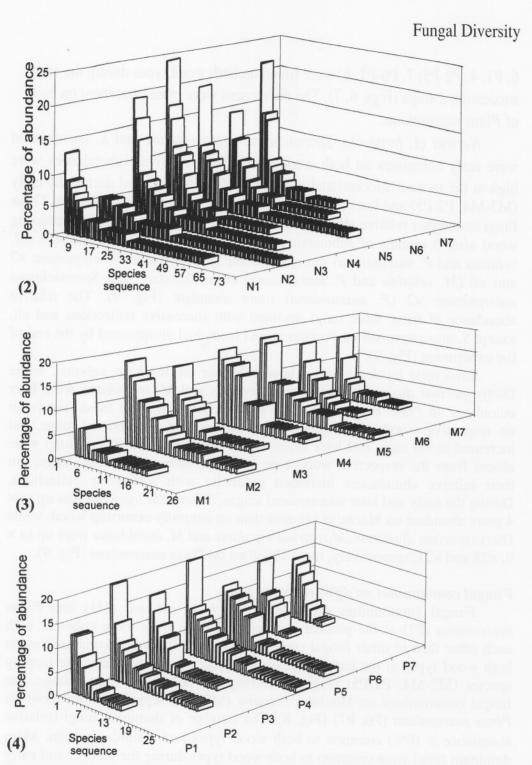
All three sets of wood samples that were collected during the cool dry season (N3, N4 and N7) formed a distinct cluster in the correspondence analysis (Fig. 5). This indicates that similar fungal communities were found during the cool dry season. Wood samples that were collected during hot wet season were scattering in the correspondence analysis (Fig. 5), indicating that during the hot wet season, fungal communities on submerged wood were variable.

Aniptodera chesapeakensis, Massarina ingoldiana and Sporoschisma nigroseptatum had high relative abundances during the cool dry seasons, but abundances declined during the hot wet seasons (Fig. 9). On the contrary, the relative abundances of Nectria cf. byssicola were higher during the hot wet season, as compared to the cool dry season (Fig. 9).

Fungal communities at different decaying stages of Machilus velutina and Pinus massoniana wood baits

Correspondence analysis of the fungal communities on baits of *Machilus velutina* and *Pinus massoniana* indicated that there were three distinct types during the 21 months submersion period (Figs. 6, 7). These three types of fungal communities are defined as the pioneer (M1; P1), early (M2-M4; P2-P5) and later (M5-M7; P6 and P7) successional groups.

Higher species richness (M1: 17, M2-M4: 18-25, M5-M7: 14-26, P1: 14, P2-P5: 19-30, P6-P7: 9) and more dominant fungi (M1: 3, M2-M4: 9, M5-M7:



Figs. 2-4. Fungal species-abundance distributions of fungal communities on different wood types. **2.** Naturally occurring wood. **3.** *Machilus velutina*. **4.** *Pinus massoniana*. Species in each sampling time are ordered with most abundant at the left to the least abundant to the right.

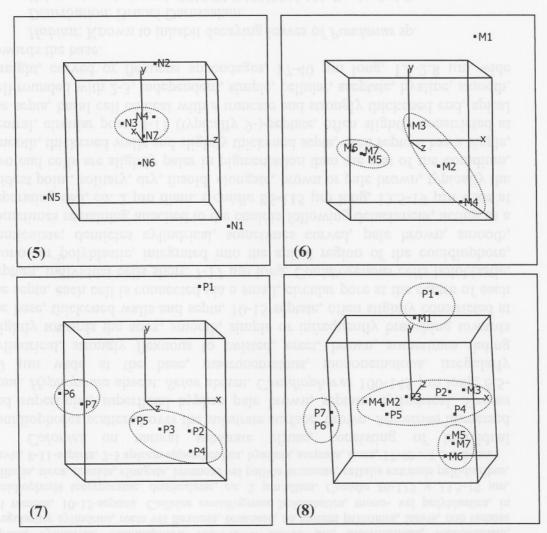
6, P1: 4, P2-P5: 7, P6-P7: 6) were found on both wood types during the early successional stage (Figs. 6, 7). The differences were more prominent on baits of *Pinus massoniana*.

Nectria cf. byssicola, Sporoschisma nigroseptatum and S. uniseptatum were early colonisers on both wood types. Their relatively abundances were high at the pioneer successional stage (M1, P1), and declined during the early (M2-M4, P2-P5) and later (M5-M7, P6, P7) successional stages (Fig. 9). These fungi had higher relative abundances on wood baits than on naturally occurring wood after 3 months of submersion: Nectria cf. byssicola: ×10 and ×16 (M. velutina and P. massoniana) more abundant; Sporoschisma nigroseptatum: ×7 and ×6 (M. velutina and P. massoniana) more abundant; and Sporoschisma uniseptatum: ×2 (P. massoniana) more abundant (Fig. 9). The relative abundance of these three fungi declined with successive collections and all, except S. nigroseptatum on P. massoniana baits, had disappeared by the end of the experiment (Fig. 9).

Savoryella lignicola was a later coloniser on Machilus velutina, while Dictyosporium digitatum, Massarina bipolaris and M. ingoldiana were later colonisers on Pinus massoniana. The relative abundances of these four fungi on respective wood types were low at the pioneer successional stage, but increased at the early and later successional stages (Fig. 9). These fungi were absent from the respective wood type at the pioneer successional stage, but their relative abundances increased gradually with successive collections. During the early and later successional stages, Savoryella lignicola was up to × 4 more abundant on Machilus velutina than on naturally occurring wood, while Dictyosporium digitatum, Massarina bipolaris and M. ingoldiana were up to × 9, ×28 and ×21, respectively, more abundant on Pinus massoniana (Fig. 9).

Fungal communities on different wood types

Fungal communities on baits of *Machilus velutina* (M1) and *Pinus massoniana* (P1) at the pioneer successional stage were more coherent with each other than to other fungal communities (Fig. 8). Fungal communities on both wood types at the early successional stage comprised many overlapping species (M2-M4, P2-P5) (Fig. 8). During the later successional stage, the fungal communities on *Machilus velutina* (M5-M7) separated from those on *Pinus massoniana* (P6, P7) (Fig. 8). The number of dominant fungi (relative abundance $\geq 10\%$) common to both wood types had a similar pattern. More dominant fungi were common to both wood types during the pioneer and early successional stages, and decreased at the later successional stage (Figs. 3, 4).

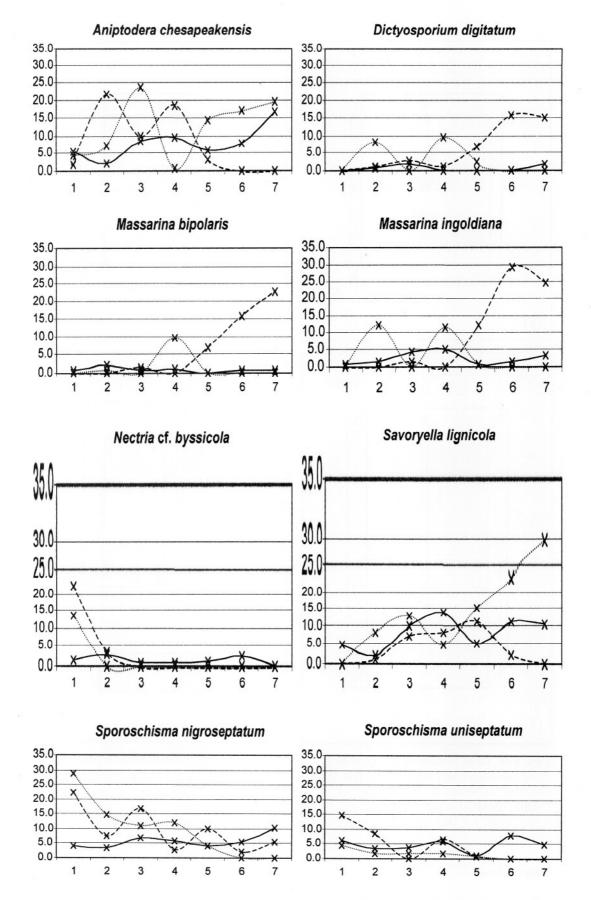


Figs. 5-8. Three dimensional correspondence ordination of fungal communities recorded on wood submerged in Tai Po Kau Forest Stream. 5. Naturally occurring wood. 6. Wood baits of *Machilus velutina*. 7. Wood baits of *Pinus massoniana*. 8. Both types of wood baits (Abbreviations: 1 = June 1996, 2 = Sep. 1996, 3 = Dec. 1996, 4 = Mar. 1997, 5 = June 1997, 6 = Sep. 1997, 7 = Dec. 1997, M = *Machilus velutina*, N = Naturally occurring wood, P = *Pinus massoniana*).

Discussion

Diversity of fungi on naturally occurring wood and baits

A higher fungal species richness was recorded in this study (175 fungi on naturally occurring wood samples and 2 types of bait by sampling 7 times from a single location) when compared to other studies. Sanders and Anderson



(1979) recorded 19 hyphomycetes on 1 type of wood using baits of different size, by sampling 5 times, over 13 weeks at 1 site. Gönczöl and Révay (1992) recorded 24 hyphomycetes on naturally occurring wood samples by sampling 6 times, over 31 months in 9 streams. Shearer and von Bodman (1983) identified 33 ascomycetes on 4 types of bait by sampling 13 times, over 30 months at 1 site. Shearer and Webster (1991) found 39 hyphomycetes on 2 types of bait by sampling twice, over 6 months at 5 sites in 1 stream, while Willoughby and Archer (1973) recorded 40 fungi on 4 types of bait by sampling 9 times, over 12 months at 1 site. Lamore and Goos (1978) found 59 fungi on naturally occurring wood samples and 2 types of bait by sampling 7 times, monthly, at 3 sites in a stream. Révay and Gönczöl (1990) also found 70 fungi on naturally occurring wood samples and 2 types of bait by sampling 8 times, over 14 months at 2 sites in a stream, while Gönczöl and Révay (1993) recorded 77 fungi on 3 types of bait by sampling 7 times, over 22 months at 2 sites in a stream. The species richness recorded in the present study is comparable to the study of Shearer and Crane (1986) who recorded 134 fungi on naturally occurring leaves and wood, and 1 type of bait by sampling monthly for 12 months at 7 sites of 6 freshwater swamps. The species richness of the present study is considerably higher than in other studies, even with limited sampling times, sampling sites and / or types of substratum.

The fungal diversity on naturally occurring wood samples was found to be higher than that on *Machilus velutina* and *Pinus massoniana* baits. This may be due to the fact that (1) fungal diversity on the baits had not reached a maximum; (2) *Machilus velutina* and *Pinus massoniana* were the only wood types used and may support a lower fungal diversity than naturally occurring wood; and (3) the baits were retrieved at intervals within less than 2 years of submersion, while naturally occurring wood samples represent an assemblage of various stages of decomposed wood, from a few weeks to several years.

A large number of fungi recorded on wood submerged in freshwater in this and other studies are infrequent taxa (e.g. Shearer and Crane, 1986; Shearer and Webster, 1991; Gönczöl and Révay, 1993).

Shearer (1972) investigated the salinity affect on fungal communities on wood submerged along a river, and recorded more species from freshwater, mostly rare species, than from estuarine water. These rare fungi accounted for the high species richness of the communities (Shearer and Webster, 1991). They may be of terrestrial origin, being washed into the streams as chance inhabitants (Shearer and Webster, 1991; Suberkropp and Krug, 1992). These rare fungi may have less of an important role, than the dominant taxa in the stream systems.

Seasonality of fungi on naturally occurring wood

Lamore and Goos (1978) noted that fungal species richness on naturally occurring wood samples submerged in a temperate stream was highest following a period of heavy rainfall. Higher fungal diversity was observed in foam and leaves after leaf fall and / or commencement of the wet season (e.g. Willoughby and Archer, 1973; Iqbal and Bhatty, 1979; Bärlocher, 1992a). A similar result was observed in this study. Higher species richness was recorded in September 1996 and June 1997 after the peak of leaf fall (March to July: Lam and Dudgeon, 1985) and heavy rainfall (Fig. 1). This may be attributed to the introduction of allochthonous detritus (providing nutrients and substrata for colonisation) and input of mycota propagules from tributaries in the surrounding area (lateral transport), and from upstream (longitudinal transport) (Bärlocher, 1992a, 1992b). In contrast, the diversity in September 1997 fell after consistent heavy rainfall from July to August, which was partly due to the El Niño event, and partly due to the Typhoons Victor and Zita. During this period of heavy rainfall, the Tai Po Kau Forest Stream was continuously flooded. Floods scour litter in the streams and deposit them on to the banks (Bell and Sipp, 1975; Mayack et al., 1989). It is probable that in the present study, wood, which had been well colonised by freshwater fungi, were washed away by the severe flooding or deposited on the banks, thus accounting for the lower fungal diversity in September 1997.

The optimal temperature for growth of species dominating temperate regions is generally between 10-20 C (Ranzoni, 1951; Tubaki, 1957; Thornton, 1963; Nilsson, 1964; Koske and Duncan, 1974; Suberkropp and Krug, 1981; Sridhar and Bärlocher, 1993; Graca and Ferreira, 1995); whereas that of the tropical species is around 25 C (Singh and Musa, 1977). The summer and winter assemblages in a North American stream (Suberkropp, 1984) and in some British streams (Iqbal and Webster, 1973, 1977) was found to respond to temperature (Suberkropp, 1984). This temperature response could also be modified by interspecific interactions (Webster *et al.*, 1976). Summer and winter assemblages of fungi were not observed in the present study. This may be attributed to the narrow temperature range in Hong Kong (average 28.8 C in July, 15.8 C in January).

Succession of fungi on Machilus velutina and Pinus massoniana baits

Fungal succession in various terrestrial (Park, 1968; Hudson, 1986) and mangrove habitats have been well documented (Tan et al., 1989, Leong et al., 1991, Hyde, 1991, Sadaba, 1995), while a study on the succession of freshwater fungi on baits of *Dipterocarpus alatus* and *Xylia dolabriformis* have been conducted by Sivichai et al. (2000). In the present study, a sequential

occurrence of three distinct fungal communities were observed on baits of *Machilus velutina* and *Pinus massoniana*: pioneer, early and later successional groups (Figs. 6, 7).

Studies on fungal succession of wood baits submerged in temperate streams yielded only five species that overlap with those found in the present study (Willoughby and Archer, 1973; Sanders and Anderson, 1979; Shearer and von Bodman, 1983; Roldán et al., 1989; Révay and Gönczöl, 1990; Shearer and Webster, 1991; Gönczöl and Révay, 1993) Seventeen species recorded by Sivichai et al. (2000) in a tropical stream in Thailand overlap with those in the present study. This makes it difficult to determine the general succession groups that individual species belong to. Shearer and von Bodman (1983) reported that in an Illinois stream, Aniptodera chesapeakensis and Arnium apiculatum were infrequent, Savoryella lignicola was abundant, but occurred sporadically, and Pseudohalonectria lignicola occurred after 6 months of submersion through to the end of the experiment (24 months). In contrast, Arnium apiculatum and Pseudohalonectria lignicola were only found on naturally occurring wood samples in the present study; while Aniptodera chesapeakensis and Savoryella lignicola were abundant, and were late colonisers of *Pinus massoniana* and *Machilus velutina* baits respectively. Willoughby and Archer (1973) reported Dictyosporium toruloides as an infrequent species, which occurred after 2 to 5 months of submersion in a small stony stream in Britain. Dictyosporium toruloides was recorded once on Pinus massoniana after 9 months of submersion in the present study.

Species common to wood baits submerged in a freshwater stream in Thailand and Tai Po Kau Forest Stream include Acrogenospora sphaerocephala, Brachydesmiella caudata, Canalisporium caribense, C. pallidum, Candelabrum brocchiatum, Dactylaria lakebarriensis, Ellisembia opaca, Helicomyces roseus, Massarina bipolaris, Montosporella setosa var. macrospora, Ophioceras dolichostomum, Phaeoisaria clematidis, Savoryella aquatica, Sporoschisma saccardoi, S. uniseptatum, Weisneriomyces javanicus, and Xylomyces chlamydosporis. None of these fungi were early or late colonisers in the Thailand study.

With the exception of *Nectria* spp., which are prominent early colonisers, species composition varied temporally, but whether they are cyclical and related to species seasonality is unknown (Shearer, 1992).

Substratum specificity

Shearer and von Bodman (1983) observed little substratum specificity in ascomycetes occurring on cherry, cottonwood, maple and sycamore baits submerged in water. Among four dominant species, *Calosphaeria* sp. was

absent on maple, *Ophioceras* sp. was absent on cherry, *Savoryella lignicola* was absent on maple and sycamore, and a bitunicate ascomycete was absent on cottonwood and cherry (Shearer and von Bodman, 1983). No substratum specificity was observed by Lamore and Goos (1978), Révay and Gönczöl (1990), Shearer and Webster (1991), and Gönczöl and Révay (1993).

In the present study, fungal communities on wood baits of *Machilus velutina* and *Pinus massoniana* were similar during both pioneer and early successional stages, but differed at the later successional stage. Among the 175 fungi found on naturally occurring wood samples, *Machilus velutina* baits and *Pinus massoniana* baits, 36 taxa occurred on all three types of substratum. These 36 taxa include the 15 dominant taxa (with relative abundance $\geq 10\%$ in at least one collecting period on any of the three types of substratum). Among the 80 taxa found on the two types of baits, 20 taxa occurred only on *Machilus velutina* baits and 21 taxa only on *Pinus massoniana* baits.

Au et al. (1992) studied the decomposition of Bauhinia purpurea leaves at the same site as in the present study. They recorded 77 taxa. With the exception that Nectria gliocladioides and a sterile mycelia (red-brown chlamydospores) that may be identical to Nectria cf. byssicola and Xylomyces chlamydosporis respectively, none of these were recorded in the present study. The difference found in the fungal communities is due to the different substrata and techniques used. Ingoldian fungi are predominant when foam, water samples, leaves and wood are incubated in aerated chambers, while non-Ingoldian fungi are found when wood is examined immediately after retrieval, or after incubation in a moist chamber (Goh and Hyde, 1996, 1999; Maltby, 1996; Chan et al., 2000; Cai et al., 2002).

There are several limitations to the present study. One has to bear in mind that fungi would have been recorded only when they sporulated. Consequently those, which did not form fruiting bodies during the period of examination, were overlooked; while others, which were present on samples in the spore form, may have formed fruiting bodies during the incubation period, and thus included in the data. Although results were correlated with climate, the influences of other factors, such as hydrology of the stream, input and output of mycota propagules, interspecific and intraspecific fungal interactions, influence of invertebrates and other organisms, together with the interactions between these factors, were not considered. Furthermore the study period was probably too short given the slow decomposition rate of both types of bait. In spite of these limitations, this study illustrates the sequential colonisation of fungi on wood submerged in the Tai Po Kau Forest Stream.

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References

- Anonymous. (1995). JMP® Statistics and graphics guide. Version 3.1 of JMP. SAS Institute Inc., Cary, NC.
- Au, D.W.T., Hodgkiss, I.J. and Vrijmoed, L.L.P. (1992). Fungi and cellulolytic activity associated with decomposition of Bauhinia purpurea leaf litter in a polluted and unpolluted Hong Kong waterway. Canadian Journal of Botany 70: 1071-1079.
- Bärlocher, F. (1992a). Community organization. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer-Verlag, Heidelberg, Berlin: 38-76.
- Bärlocher, F. (1992b). Recent developments in stream ecology and their relevance to aquatic mycology. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer-Verlag, Heidelberg, Berlin: 16-37.
- Bell, D.T. and Sipp, S.K. (1975). The litter stratum in the streamside forest ecosystem. Oikos 26: 391-397.
- Booth, T. and Kenkel, N. (1986). Ecological studies of lignicolous marine fungi: a distribution model based on ordination and classification. In: *The Biology of Marine Fungi* (ed. S.T. Moss). Cambridge University Press: 297-310.
- Cai, L., Tsui, C.K.M., Zhang, K. and Hyde, K.D. (2002). Freshwater fungi from Lake Fuxian, Yunnan, China. Fungal Diversity 9: 57-70.
- Chan, S.Y. (2000). Ingoldian fungi in Lam Tsuen River and Tai Po Kau Forest Stream, Hong Kong. Fungal Diversity 5: 109-118.
- Dudgeon, D. (1982). Aspects of the hydrology of Tai Po Kau Forest Stream, New Territories, Hong Kong. Archiv fur Hydrobiologie Supplement 64: 1-35.
- Dudgeon, D. (1992). Patterns and Processes in Stream Ecology: A Synoptic Review of Hong Kong Running Waters. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany.
- Goh, T.K. and Hyde, K.D. (1996). Biodiversity of freshwater fungi. Journal of Industrial Microbiology 17: 328-345.
- Goh, T.K. and Hyde, K.D. (1999). Fungi on submerged wood and bamboo in the Plover Cove Reservoir, Hong Kong. Fungal Diversity 3: 57-85.
- Gönczöl, J. and Révay, A. (1992). Aquatic hyphomycetes in softwater and hardwater streams of the Aggtelek National Park, NE Hungary. Annales Historico-Naturales Musei Nationalis Hungarici 84: 17-31.
- Gönczöl, J. and Révay, Á. (1993). Further studies on fungal colonizations of twigs in the Morgó-stream, Hungary. Nova Hedwigia 56: 531-542.
- Government of Hong Kong (1982). *Tai Po Kau Special Area*. Hong Kong Country Park Authority.
- Government of the Hong Kong SAR (1998). Hong Kong Observatory. http://www.info.gov.hk/hko/wxinfo.
- Graca, M.A.S. and Ferreira, R.C.F. (1995). The ability of selected aquatic hyphomycetes and terrestrial fungi to decompose leaves in freshwater. Sydowia 47: 167-179.
- Hudson, H.J. (1986). Fungal Biology. Cambridge University Press, London.
- Hyde, K.D. (1991). Fungal colonization of *Rhizophora apiculata* and *Xylocarpus granatum* poles in Kampong Kapok mangrove, Brunei. Sydowia 43: 31-38.

- Iqbal, S.H. and Bhatty, S.F. (1979). Conidia from stream foam. Transactions of the Mycological Society of Japan 20: 83-91.
- Iqbal, S.H. and Webster, J. (1973). Aquatic hyphomycete spora of the River Exe and its tributaries. Transactions of the British Mycological Society 61: 331-346.
- Iqbal, S.H. and Webster, J. (1977). Aquatic hyphomycete spora of some Dartmoor streams. Transactions of the British Mycological Society 65: 233-241.
- Koske, R.E. and Duncan, I.W. (1974). Temperature effects on growth, sporulation and germination of some "aquatic hyphomycetes". Canadian Journal of Botany 52: 1387-1391.
- Lam, P.K. and Dudgeon, D. (1985). Seasonal effects on litterfall in Hong Kong mixed forest. Journal of Tropical Ecology 1: 55-64.
- Lamore, B.J. and Goos, R.D. (1978). Wood-inhabiting fungi of a freshwater stream in Rhode Island. Mycologia 70: 1025-1034.
- Leong, W.F., Tan, T.K. and Jones, E.B.G. (1991). Fungal colonization of submerged *Bruguiera cylindrica* and *Rhizophora apiculata* wood. Botanical Marina 34: 69-76.
- Maltby, L. (1996). Heterotrophic Microbes. In: *River Biota: Diversity and Dynamics Selected Extracts from the Rivers Handbook* (eds. G. Petts and P. Calow). Oxford, Blackwell Science: 45-74.
- Mayack, D.T., Thorp, J.H. and Cothran, M. (1989). Effects of burial and floodplain retention on stream processing of allochthonous litter. Oikos 54: 378-388.
- Nicholson, B. (1994). Tai Po Kau: Past, Present and Future. EcoScene 1: 2.
- Nilsson, S. (1964). Freshwater hyphomycetes: taxonomy, morphology and ecology. Symbolae Botanicae Upssalienses 182: 1-130.
- Park, D. (1968). The ecology of terrestrial fungi. In: *The Fungi* (eds. G.C. Ainsworth and A.S. Sussman). Academic Press, New York: 103-112.
- Ranzoni, F.V. (1951). Nutrient requirements for two species of aquatic Hyphomycetes. Mycologia 43: 130-141.
- Révay, Á. and Gönczöl, J. (1990). Longitudinal distribution and colonization pattern of wood-inhabiting fungi in a mountain stream in Hungary. Nova Hedwigia 51: 505-520.
- Roldán, A., Puig, M.A. and Honrubia, M. (1989). Fungal communities associated with wood test-blocks in a Mediterranean stream. Annales de Limnologie 25: 191-195.
- Sadaba, R.B., Vrijmoed, L.L.P., Jones, E.B.G. and Hodgkiss, I.J. (1995). Observations on vertical distribution of fungi associated with standing senescent *Acanthus ilicifolius* stems at Mai Po Mangrove, Hong Kong. Hydrobiologia 295: 119-126.
- Sanders, P.F. and Anderson, J.M. (1979). Colonization of wood blocks by aquatic hyphomycetes. Transactions of the British Mycological Society 73: 103-107.
- Shearer, C.A. (1972). Fungi of the Chesapeake Bay and its tributaries. III. The distribution of wood-inhabiting ascomycetes and fungi imperfecti of the Patuxent River. American Journal of Botany 59: 961-969.
- Shearer, C.A. (1992). The role of woody debris. In: *The Ecology of Aquatic Hyphomycetes* (ed. F. Bärlocher). Springer-Verlag, Heidelberg, Berlin: 77-98.
- Shearer, C.A. and Crane, J.L. (1986). Illinois fungi XII. Fungi and myxomycetes from wood and leaves submerged in southern Illinois swamps. Mycotaxon 25: 527-538.
- Shearer, C.A. and von Bodman, S.B. (1983). Patterns of occurrence of ascomycetes associated with decomposing twigs in a midwestern stream. Mycologia 75: 518-530.
- Shearer, C.A. and Webster, J. (1991). Aquatic hyphomycete communities in the River Teign. IV. Twig colonization. Mycological Research 95: 413-420.

- Singh, N. and Musa, T.M. (1977). Terrestrial occurrence and the effect of temperature on growth, sporulation and spore germination of some tropical aquatic hyphomycetes. Transactions of the British Mycological Society 68: 103-106.
- Sivichai, S., Jones, E.B.G. and Hywel-Jones, N.L. (2000). Fungal colonisation of wood in a freshwater stream at Khao Yai National Park, Thailand. Fungal Diversity 5: 71-88.
- Sridhar, K.R. and Bärlocher, F. (1993). Effect of temperature on growth and survival of five aquatic hyphomycetes. Sydowia 45: 377-387.
- Suberkropp, K. (1984). Effect of temperature on seasonal occurrence of aquatic hyphomycetes. Transactions of the British Mycological Society 82: 53-62.
- Suberkropp, K. and Krug, M.J. (1981). Degradation of leaf litter by aquatic hyphomycetes. In: *The Fungal Community: Its Organization and Role in the Ecosystem* (eds. D.T. Wicklow and G.C. Carroll). Marcel Dekker Press, New York: 761-776.
- Suberkropp, K. and Krug, M.J. (1992). Aquatic hyphomycete communities. In: *The Fungal Community: Its Organization and Role in the Ecosystem* (eds. D.T. Wicklow and G.C. Carroll). 2nd edn. Marcel Dekker Press, New York: 729-747.
- Tan, T.K., Teng, C.L. and Jones, E.B.G. (1989). Succession of fungi on wood of *Avicennia* alba and *A. lanata* in Singapore. Canadian Journal of Botany 67: 2686-2691.
- Thornton, D.R. (1963). The physiology and nutrition of some aquatic hyphomycetes. Journal of General Microbiology 33: 23-31.
- Tubaki, K. (1957). Studies on the Japanese hyphomycetes III. Aquatic group. Bulletin of National Science Museum (Tokyo) 41: 249-268.
- Webster, J., Moran, S.T. and Davey, R.A. (1976). Growth and sporulation of *Tricladium chaetocladium* and *Lunulospora curvula* in relation to temperature. Transactions of the British Mycological Society 67: 491-495.
- Willoughby, L.G. and Archer, J.F. (1973). The fungal spora of a freshwater stream and its colonization patter on wood. Freshwater Biology 3: 219-239.
- Yanna, Ho, W.H. and Hyde, K.D. (2002). Fungal succession on fronds of *Phoenix hanceana* in Hong Kong. In: *Fungal Succession* (eds. K.D. Hyde and E.B.G. Jones). Fungal Diversity 10: 183-209.

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