Fungi colonising and sporulating on submerged wood in the River Severn, UK

David F. Kane[1], W.Y. Tam[2] and E.B. Gareth Jones[3*]

[1]School of Biological Sciences, University of Portsmouth, King Henry 1st Street, PO1 2DY, Portsmouth, UK
[2]Department of Biology and Chemistry, City University of Hong Kong, 83 Tat Chee Avenue, Kowloon, Hong Kong SAR, PR China
[3]BIOTEC, National Center for Genetic Engineering and Biotechnology, 113 Paholyothin Road, Klong 1, Klong Luang, Pathumthani 12120, Thailand

Kane, D.F., Tam, W.Y. and Jones, E.B.G. (2002). Fungi colonising and sporulating on submerged wood in the River Severn, UK. In: *Fungal Succession* (eds. K.D. Hyde and E.B.G. Jones). Fungal Diversity 10: 45-55.

Test blocks of *Fagus sylvatica* and *Pinus sylvestris* were submerged in the River Severn, England, UK, for 92 weeks and recovered at frequent intervals. Recovered samples were incubated in moist chambers and sporulating fungi on the test blocks were recorded. Fifty fungi consisting of 35 anamorphic species, 13 Ascomycota and 2 Basidiomycota were identified. Species diversity (40) was greatest on the beech test blocks, while only 28 species occurred on the Scots pine test blocks. The most common fungi on beech were *Camposporium pellucidum*, *Dictyochaeta parva*, *Pseudohalonectria lignicola* (each with 95% occurrence) and *Trichocladium lignicola* (89%). On Scots pine *T. lignicola* occurred on 95% of the test blocks. A succession of sporulating fungi was observed on the wood over a 3 month incubation period in the laboratory. The results are compared with other studies on lignicolous aquatic fungi from temperate and tropical locations. These indicate that different fungal communities occur in different geographical locations.

Key words: anamorphic fungi, Ascomycota, Basidiomycota, biodiversity, ecology, lignicolous fungi, stream, wood.

Introduction

Most studies of lignicolous freshwater fungi have concentrated on submerged, trapped natural wood in streams and rivers (Willoughby and Archer, 1973; Hyde and Goh, 1997, 1998, 1999; Goh and Hyde, 1999; Tsui *et al*., 2000). Jones and Oliver (1964) however, pioneered the exposure of test blocks in rivers and their retrieval at fixed intervals, thus enabling the documentation of the sequential colonisation of fungi on woody material by observing their sporulation. This was developed further by Eaton and Jones (1971a,b) in their paper on the colonisation of pine and beech test blocks in

* Corresponding author: E.B. Gareth Jones; email: bhgareth@yahoo.com

water cooling towers and intake water from the River Dee. Sanders and Anderson (1979) also used this approach in examining the effect of resource size on the biodiversity of colonising fungi. Examination of naturally trapped wood and submerged timbers have also been applied to study fungal diversity in a tropical river in Thailand, with naturally trapped wood yielding a greater fungal diversity (Sivichai *et al.*, 2000).

While many studies have documented the lignicolous freshwater fungi in tropical and subtropical locations, few have followed the colonisation of wood in temperate or tropical climates (Jones, 1981; Shearer and Bodman, 1983; Révay and Gönczöl, 1990; Hyde and Goh, 1999). Currently, some 1000 lignicolous freshwater fungi have been documented (Wong *et al.*, 1998; Sivichai and Hywel-Jones, 1999; Sivichai *et al.*, 2000; Ho *et al.*, 2001) and further new species await description. Our study was undertaken in order to document the sequence of sporulation / colonisation of fungi on wood submerged in the River Severn, southern England and to compare species composition with a previous study by Eaton and Jones (1971a,b) in the River Dee.

Materials and methods

Location of the experimental site

The River Severn has its source in the Cambrian Mountains, Wales and is one of Britain's largest river systems, with three main tributaries, the Stour, Teme and Avon. The Mythe water treatment work, part of the Severn-Trent Water Authority, is situated between the main Tewkesbury to Hereford Road (A438) and the River Severn just outside Tewkesbury. From a point upstream of the junction with the River Avon, the Water Authority abstracts up to 109×10^3 cubic meters per day. A Severn Water Authority jetty on the River Severn was used for the exposure of test blocks.

Exposure of wood samples

Test blocks 15 × 7.5 × 1.9 cm of beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*), quarter-sawn seasoned sapwood and planed smooth on all faces, with a 1.3 cm diam. hole bored through the centre of each were used. Blocks were strung together on 2 cm plastic rope (Courlene), 10 cm apart. Pairs of beech and pine blocks were alternately threaded on each rope, and 12 ropes completely submerged in the River Severn. One set of blocks was removed after 6, 12, 19, 26, 33, 57, 62, 73 and 92 weeks, respectively.

Recovery and incubation of test blocks

On removal, each set of blocks was placed in a sterile bag (Sterilin) for transportation to the laboratory, when each block was scraped with a sterile glass slide, to remove surface detritus and placed in a clean sterile bag. Cold autoclaved distilled water (500 ml) was added and the bag shaken vigorously to remove silt particles adhering to the blocks. These were then incubated on sterile tissue paper in an ethanol sterilized plastic sandwich box (Jones, 1971). Incubation was at room temperature (~ 20 C) under natural light conditions. Test samples were examined after 2 days and 1, 4 and 12 weeks of incubation. Fungi sporulating on the wood were recorded and voucher slides prepared and are held at the School of Biological Sciences, University of Portsmouth.

Results

A total of 50 fungal taxa were recorded, consisting of 35 anamorphic fungi (representing 70% of all taxa identified), 13 Ascomycota (26%) and 2 Basidiomycota (4%) (Table 1). Species diversity was greatest on the beech test blocks (40), while only 28 species occurred on the pine wood. *Pseudohalonectria lignicola* and *Ophioceras dolichostomum* colonised, respectively, 17 and 12 beech blocks, but each occurred only once on the pine blocks. Of the anamorphic fungi, *Camposporium pellucidum* colonised 17 beech test blocks, but only 3 pine blocks, while *Clavariopsis aquatica, Dactyella aquatica, Paecilomyces elegans, Wardomyces anomalus* and 18 others occurred only on beech. Conversely, *Alatospora acuminata, Campylospora chaetocladia, Sterigmatobotrys macrocarpa, Trichocladium alopallonellum* and five others were only found on pine. Other fungi showed less substrate specificity, e.g. *Trichocladium lignicola* occurred on 17 pine and 16 beech test blocks. Fungi with a percentage occurrence of 75% and above were more common on beech (*Camposporium pellucidum, Dictyochaeta parva, Pseudohalonectria lignicola, Trichocladium lignicola*), with only *T. lignicola* on pine.

Table 2 lists the sequential appearance and loss of sporulating structures of eleven of the most common fungi encountered on the test blocks. Aquatic hyphomycetes sporulated on wood on retrieval and sporulated profusely for up to 48 hours to 1 week, then ceased fruiting, while the dematiaceous species (*Camposporium pellucidum, Trichocladium alopallonellum, T. lignicola*) were present throughout the incubation period. Most other fungi were not sporulating upon retrieval from the river (e.g. *Trematosphaeria pertusa, Massarina* sp.), but fruited after incubation.

Table 3 lists the frequent fungi colonising beech and pine test blocks, with their percentage occurrence, in descending order. Most fungi had a high frequency of occurrence, e.g. *Camposporium pellucidum, Dictyochaeta parva* and *Pseudohalonectria lignicola* (each with 95% frequency of occurrence).

Table 1. Fungi sporulating on submerged beech and Scots pine test blocks in the River Severn.

Species	**River Severn**	
	Beech	**Pine**
Alatospora acuminata Ingold	-	4
Anguillospora crassa Ingold	5	2
Anguillospora longissima (Sacc. & Syd.) Ingold	3	1
Arthrobotrys oligospora Fresen.	2	1
Camposporium pellucidum (Grove) S. Hughes	17	3
Campylospora chaetocladia Ranzoni	-	3
Cephalosporium sp.	-	1
Chaetomium globosum Kunze ex Fries	4	-
Clavariopsis aquatica de Wild.	2	-
Culicidospora gravida Petersen	-	2
Dactylium sp.	3	-
Dactylella aquatica (Ingold) Ranzoni	3	-
Dendryphion nanum (Nees ex Gray) S. Hughes	1	-
Dictyochaeta parva (S. Hughes & W.B. Kendr.) Hol.-Jech.	17	6
Dictyosporium toruloides (Corda) Guég.	4	-
Doratomyces purpureofuscus (Schwein.) Morton & Smith	1	-
Flagellospora sp.	1	1
Fusarium sp.	13	7
Geotrichum sp.	1	-
Graphium calicioides (Fr.) Cooke & Massee	1	2
Helicomyces scandens Morgan	3	-
Heliscus lugdunensis Sacc. & Terry [= *Nectria lugdunensis*]	3	7
Lasiosordaria lignicola (Fuckel) Chenant.	6	2
Lulworthia sp.	-	1
Macrophoma sp.	1	-
Margaritispora aquatica Ingold	1	-
Massarina sp.	1	1
Melanospora sp.	1	-
Monodictys sp.	-	1
Nectria lugdunensis Webster [= *Heliscus lugdunensis*]	1	-
Nais inornata Kohlm.	2	2
Ophioceras dolichostomum (Berk. & M.A. Curtis) Sacc.	12	1
Paecilomyces elegans (Corda) E.W. Mason & S. Hughes	6	-
Phoma sp.	1	1
Pleospora sp.	1	-
Pleurophragmium simplex (Berk. & Broome) S. Hughes	1	1
Pseudohalonectria lignicola Minoura & T. Muroi	17	1
Rosellinia sp.	1	-
Sterigmatobotrys macrocarpa (Corda) S. Hughes	-	3
Torula herbarum (Pers.) Link ex S.F. Gray	1	-
Trematosphaeria pertusa (Pers. ex Fries) Fuckel	7	1
Trichocladium alopallonellum (Myers & R.T. Moore) Kohlm. & Volkm.-Kohlm.	-	4

Table 1 continued.

Fungus	River Severn	
	Beech	Pine
Trichocladium lignicola I. Schmidt	16	17
Trichoderma sp.	1	-
Tricladium splendens Ingold	1	-
Verticillium sp.	-	1
Wardomyces anomolus F.T. Brooks & Hansf.	3	-
Unidentified ascomycete	-	1
Basidiomycete mycelium	2	
Basidiomycete, Agaricales	1	-
Total fugal occurrences	168	78
Total test blocks	18	18
Number of species recorded	40	28
Number of species on 75% or more blocks	4	1
Mean dry weight (gms) of last four sets of blocks (98% confidence limits shown in brackets)	84.4 (± 3.2)	77.7 (± 6.9)

Table 2. Incubation time recorded for the loss, or appearance, of sporulating structures for eleven frequent fungi.

Fungus	Incubation time necessary for the loss or appearance of sporulating structures				
	On removal	48 hours	1 week	1 month	3 months
Heliscus lugdunensis	+	+	-	-	-
Alatospora acuminata	+	+	+	-	-
Trichocladium alopallonellum	+	+	+	+	+
Trichocladium lignicola	+	+	+	+	+
Camposporium pellucidum	-	+	+	+	+
Dictyochaeta parva	-	+	+	+	+
Ophioceras dolichostomum	-	-	+	+	+
Peyronelina glomerulata	-	-	+	+	+
Trematosphaeria pertusa	-	-	+	+	+
Massarina sp.	-	-	-	+	+
Melanospora sp.	-	-	-	-	+

Wood decay was evident, especially after 92 weeks submergence, and examination of timber showed significant soft rot decay.

Discussion

Various ecological descriptions have been proposed for aquatic fungi. Cooke (1976) divided them into hydro- and geo- fungi, the former largely stramenopilous organisms, the latter typically soil fungi. Park (1972) introduced the terms indwellers (constant activity), migrants (periodic or

Table 3. Frequent fungi colonising beech and Scots pine test blocks.

Beech	Percentage occurrence	Scots pine	Percentage occurrence
Camposporium pellucidum	95	*Trichocladium lignicola*	95
Dictyochaeta parva	95	*Fusarium* sp.	39
Pseudohalonectria lignicola	95	*Heliscus lugdunensis*	39
Trichocladium lignicola	89	*Dictyochaeta parva*	33
Fusarium sp.	72		
Ophioceras dolichostomum	67		
Trematosphaeria pertusa	39		
Lasiosordaria lignicola	33		
Paecilomyces elegans	33		

Table 4. A comparison of the four most common freshwater lignicolous fungi in each of the selected studies (Percentage frequency of occurrence).

Hyde *et al.*, 1998		Tsui *et al.*, 2000		Sivichai *et al.*, 2000		Present study	
Nais aquatica	34	*Aniptodera chesapeakensis*	2-30	*Savoryella aquatica*	90	*Camposporium pellucidum*	95
Ophioceras sp.	22	*Candelabrum brocchiatum*	8-24	*Helicomyces roseus*	63	*Dictyochaeta parva*	95
Annulatascus velatisporus	15	*Sporoschisma uniseptatum*	8-24	*Ellisembia opaca*	62	*Pseudohalonectria lignicola*	95
Kirschsteiniothelia elaterascus	12	*Helicosporium griseum*	12-24	*Biflagellospora siamensis*	54	*Trichocladium lignicola*	89

sporadic activity), versatiles (sporadic activity) and transients (those exhibiting no activity). However, he pointed out that "there may be no simple and exclusive division of micro-organisms into aquatic and non-aquatic types, rather there may be two extreme ends of a complete spectrum".

The depth of water in most freshwater systems is rarely constant. The water level in the River Severn frequently fluctuates by more than 180 cm. Indeed many freshwater streams will completely dry out at certain times of the year (Hyde and Goh, 1997; Sivichai *et al.,* 2000). This fluctuation in water level will lead to a natural situation whereby a substratum may only spend part or a limited time in the water and for the rest be exposed to air. This is probably more often the case for timber than for allochthonous leaves that are degraded much faster (Jones, 1981). This terrestrial state may be important when naturally trapped wood is studied (Ho *et al.*, 2001), e.g. discomycete teleomorphs that generally eject their ascopores. The timbers used in this study were weighed down to ensure continued submergence, so that the fungi recorded colonised the wood during this exposure period.

Species diversity

Fifty taxa were recorded in this study. This compares with: 59 in the Saugatucket river, Rhode Island (Lamore and Goos, 1978); 34 on beech, 20 on pine in the River Dee, England (Eaton and Jones, 1971b); 58 in the Palmiet River, South Africa (Hyde *et al.*, 1998); 53 on *Dipterocarpus alatus*, 62 on *Xylia dolabriformis* in streams in Khao Yai National Park, Thailand (Sivichai, *et al.*, 2000) and to 153 in various streams in Hong Kong (Tsui, *et al.*, 2000).

In the study by Eaton and Jones (1971b) on the River Dee, identical procedures were used as in this study. However, there were significant differences in the types of fungi recorded. At the River Dee the most frequent fungi were: *Clasterosporium caricinum*, *Helicoon sessile* and *Monodictys putredinis*; in this study they were: *Camposporium pellucidum*, *Dictyochaeta parva*, *Pseudohalonectria lignicola* and *Trichocladium lignicola*. Some fungi however were common to both studies: *Chaetomium globosum*, *Dictyochaeta parva*, *Nais inornata*, *Trematosphaeria pertusa* and *Trichocladium alopallonellum*. There was some overlap in the species collected in the River Severn with those listed by Shearer and von Bodman (1983) from twigs submerged in Jordan Creek, Illinois, e.g. *Pseudohalonectria lignicola* (frequency of occurrence 53%), *Nais inornata*, *Trichocladium lignicola* and *Ophioceras* species. Hyde and Goh (1999) recorded 25 species on submerged wood in the River Coln, Cotswolds, UK. While a few were common to this study, the majority differed significantly, with the most frequent species being: *Cryptosporiopsis* sp. (6%), *Ascotaiwania pallida* and *Septotrullula bacilligera* (5%) (Hyde and Goh, 1999).

In comparing the lignicolous fungi occurring in tropical / subtropical locations with those from temperate areas there is little overlap in the common species. Table 4 shows the four most common species in four selected studies. There is no overlap in the most common species recovered. Noteworthy is the observation that the percentage frequency of occurrence of species colonising artificial wood baits (Sivichai *et al.*, 2000, and present study) is significantly higher than for naturally collected wood (Hyde *et al.*, 1998; Tsui *et al.*, 2000). This may be accounted for in a number of ways. For naturally occurring wood the period of submergence is not known, thus early colonisers may not be recovered. For example, aquatic hyphomycetes may only occur on the wood for relatively short periods as demonstrated in this study (Table 2). On naturally occurring wood that has been in the water for a long time, only the climax communities may be present (Tsui *et al.*, 2000).

In our study we examined the test blocks on return to the laboratory, at 48 hours and at one week while there was still a film of water on the wood surface. During this period a number of Ingoldian hyphomyctes sporulated on the wood. These are rarely recorded on incubated wood and it is possible that the samples are not examined early enough. Jones and Oliver (1964) also made the same observation, while Kirk (1969) suggested wood panels should be vigorously aerated in water. Using this method he isolated the hyphomcyete *Clavatospora stellatacula.*

Great variation in species diversity at different locations has been noted in other studies, such as between two streams within the same National Park in Thailand (Sivichai, pers. comm.). In Hong Kong, Tsui *et al.* (2000) compared the fungal communities sporulating on wood collected in five different streams. The fungal community in the stream on Lantau Island was distinct from those at four streams in the New Territories. They attributed this to the paucity of tree vegetation surrounding the stream at Lantau.

Variation exists in the composition of the dominant fungi recorded from wood in freshwater habitats. In the present study, anamorphic fungi were prevalent (70%). Similar results have been obtained by: Sivichai *et al.* (2000): 77% anamorphic species on *Xylia dolabriformis*, 70% on *Dipterocarpus alatus*; Tsui *et al.* (2000): 60%, and Lamore and Goos (1978): 72%, while Hyde and Goh (1997) and Hyde *et al.* (1998) report a slightly higher number of ascomycetes than hyphomycetes (28:22; 30:22), respectively.

Only six aquatic hyphomycetes (Ingoldian fungi; *sensu* Ingold, 1975) occurring in this study were found on either timber sufficiently frequently to be considered of significance, with *Heliscus lugdunensis* (present as the anamorph), sporulating on 39% of the pine and 17% on beech test blocks, being the most common. Ingoldian hyphomycetes have also been regularly recorded from submerged wood by other workers (Jones and Oliver, 1964; Eaton, 1969; Eaton and Jones. 1971b; Willoughby and Archer, 1973; Lamour and Goos, 1978; Tsui *et al.*, 2000). However, they have never been found to occur as the dominant species on woody material. This may be due to their inability to degrade lignocellulose, although Jones (1981) and Shearer and Zare-Maivan (1988) have shown they can cause soft rot decay of wood. Other reasons for their paucity is that they may not be able to compete with other fungi in the capture and colonisation of a resource or their sporulation is inhibted by other fungi.

Comparatively few of the aquatic hyphomycetes (Ingoldian fungi), common on decomposing deciduous leaves in freshwater, have been observed on lignicolous substrata (Eaton and Jones, 1971a,b; Lamore and Goos, 1978; Hyde *et al.*, 1998; Sivichai *et al.*, 2000; Tsui *et al.*, 2000). By the use of incubation techniques more favourable for their sporulation (e.g. submerged in aerated chambers, Sanders and Anderson 1979), it is likely that more species would be recovered from woody substrata and a greater consideration given to their ligno-cellulolytic ability and role in nature.

A large number of infrequently observed fungal species, most of which are common soil or litter fungi, fall into an infrequent or rare group. Individually they are probably not responsible for much activity in the aquatic environment. Recent studies (Sivichai *et al.*, 2000; Tsui *et al.*, 2000) have shown a preponderance of anamorphic fungi on submerged wood, some previously regarded as aero-aquatics of decaying leaves (Fisher, 1977), litter-inhabiting fungi (Kuthubutheen and Nawawi, 1993) and soil fungi (Domsch, *et al.*, 1980). Although these anamorphic fungi have been reported from other substrata / habitats, they clearly have the ability to settle, attach and colonise woody substrata in freshwater habitats, often under turbulent conditions. How active they are in the decay of wood remains to be determined.

No discomycetes were recovered on the test blocks and this is in common with other investigations (Eaton and Jones, 1971a,b; Hyde *et al.*, 1998; Sivichai *et al.*, 2000; Tsui *et al.*, 2000). The discomycete teleomorph rarely develops when the substratum is permanently submerged, but the anamorph can appear under these conditions. For example, Sivichai (2000) reported *Hymenoscyphus varicosporoides* on incubation of test blocks, while the anamorph (a *Tricladium* sp.) has been found sporulating soon after recovery. Discomycetes prefer an amphibious habitat as demonstrated by the number colonising phanerogams growing in water in temperate locations (Shearer, 1993).

Jones (2000) reviewed the effect of various factors on the colonisation of wood in the marine environment. However this study, in common with others, has shown that we know little about the factors that control fungal diversity in freshwater habitats. Greater attention to the effects of river water chemistry, the temperature, of the shading effect of the tree canopy over the stream, of the abundance of decaying wood in the river, of water runoff from adjoining leaf litter, which can affect fungal propagules available for colonisation, of interference competition between fungi and water velocity, are all factors that may play a role in determining the observed biodiversity.

Acknowledgements

D.F. Kane is greatful to the University of Portsmouth for the award of a research scholarship. We thank K.D. Hyde and J. Webster for their invaluable comments on an early draft of this paper.

References

Cooke, W.B. (1976). Fungi in sewage. In: *Recent Advances in Aquatic Mycology* (ed. E.B.G. Jones). Elek Science: 289-434.

Domsch, K.H., Gams, W. and Anderson, T.H. (1980). *Compendium of Soil Fungi, Vol. I and II*. Academic Press, London.

Eaton, R.A. (1969). *The Biodeterioration of Timber in Water Cooling Towers*. Ph.D. Thesis, CNNA.

Eaton, R.A. and Jones, E.B.G. (1971a). The biodeterioration of timber in water cooling towers I. Fungal ecology and the decay of wood at Connah's Quay and Ince. Material und Organism 6: 51-80.

Eaton, R.A. and Jones, E.B.G. (1971b). The biodeterioration of timber in water cooling towers II. Fungi growing on wood in different positions in a water cooling system. Material und Organism 6: 81-92.

Fisher, P.J. (1977). *Ecological Studies on Aero-aquatic Hyphomycetes*. Ph.D. Thesis, University of Exeter.

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.

Ho, W.H., Hyde, K.D., Hodgkiss, I.J. and Yanna. (2001). Fungal communities on submerged wood from streams in Brunei, Hong Kong, and Malaysia. Mycological Research 105: 1492-1501.

Hyde, K.D. and Goh, T.K. (1997). Fungi on submerged wood in a small stream on Mt. Lewis, North Queensland, Australia. Muelleria 10: 145-157.

Hyde, K.D. and Goh, T.K. (1998). Fungi on submerged wood in Lake Barrine, North Queensland, Australia. Mycological Research 102: 739-749.

Hyde, K.D. and Goh, T.K. (1999). Fungi on submerged wood in the River Coln, the Cotswolds, UK. Mycological Research 103: 1561-1574.

Hyde, K.D., Goh, T.K. and Steinke, T.D. (1998). Fungi on submerged wood in the Palmiet River, Durban, South Africa. South Africa Journal Botany 64: 151-162.

Ingold, C.T. (1975). An illustrated guide to aquatic and water-borne Hyphomyctes (Fungi Imperfecti) with notes on their biology. Freshwater Biological Association, Science publications 30: 1-96.

Jones, E.B.G. (1971). Aquatic fungi. In: *Methods in Microbiology, Vol. 4* (ed. C. Booth). Academic Press, New York: 335-365.

Jones, E.B.G. (1981). Observations on the ecology of lignicolous 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: 731-742.

Jones, E.B.G. (2000). Marine fungi: some factors influencing biodiversity. Fungal Diversity 4: 53-73.

Jones, E.B.G. and A.C. Oliver (1964). Occurrence of aquatic hyphomycetes on wood submerged in fresh and brackish water. Transactions of the British Mycological Society 47: 45-48.

Kirk, P.W. (1969). Isolation and culture of lignicolous marine fungi. Mycologia 61: 174-177.

Kuthubutheen, A.J. and Nawawi, A. (1993). Three new and several interesting species of *Sporidesmiella* from submerged litter in Malaysia. Mycological Research 97: 1305-1314.

Lamore, B.J. and Goos, R.D. (1978). Wood-inhabiting fungi of a freshwater stream in Rhode Island. Mycologia 70: 1025-1034.

Park, D. (1972). On the ecology of heterotrophic microorganisms in freshwater. Transactions of the British Mycological Society 58: 291-299.

Révay, A. and Gönczöl, J. (1990). Longitudinal distribution and colonization patterns of wood-inhabiting fungi in a mountain stream in Hungary. Nova Hedwigia 51: 505-520.

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. (1993). The freshwater ascomycetes. Nova Hedwigia 56: 1-33.

Shearer, C.A. and von Bodman, S. (1983). Pattern of occurrence of ascomycetes associated with decomposing twigs in a mid-western stream. Mycologia 75: 518-530.

Shearer, C.A. and Zare-Maivan, H. (1988). *In vitro* hyphal interactions among wood and leaf-inhabiting Ascomycetes and Fungi imperfecti from freshwater habitats. Mycologia 8: 31-37.

Sivichai, S. (2000). *Tropical Freshwater Fungi: Their Ecology and Taxonomy*. Ph.D. Thesis, University of Portsmouth.

Sivichai, S. and Hywel-Jones, N.L. (1999). *Biflagellospora* aero-aquatic hyphomycetes from submerged wood in Thailand. Mycological Research 103: 908-914.

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. Aquatic Mycology Across the Millennium. Fungal Diversity 5: 71-88.

Tsui, C.K.M., Hyde, K.D. and Hodgkiss, I.J. (2000). Biodiversity of fungi on submerged wood in Hong Kong streams. Aquatic Microbiological Ecology 21: 289-298.

Willoughby, L.G. and Archer, J.F. (1973). The fungal flora of a freshwater stream and its colonization pattern on wood. Freshwater Biology 3: 219-239.

Wong, M.K.M., Goh, T.K., Hodgkiss, I.J., Hyde, K.D., Ranghoo, V.M., Tsui, C.K.M., Ho, W.H., Wong, S.W. and Yuen, T.K. (1998). Role of fungi in freshwater ecosystem. Biodiversity and Conservation 7: 1187-1206.

(Received 4 April 2002; accepted 30 May 2002)