Mycoscience (2010) 51:104–115
DOI 10.1007/s10267-009-0017-z

FULL PAPER

Wood-inhabiting filamentous fungi in 12 high-altitude streams of the Western Ghats by damp incubation and bubble chamber incubation

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Received: 26 March 2009 / Accepted: 27 August 2009 / Published online: 20 January 2010

Abstract The diversity and distribution of fungi on naturally submerged wood from 12 high-altitude streams of the Western Ghats in India were studied by damp chamber incubation and bubble chamber incubation. The damp chamber incubation of wood samples yielded 29 fungal taxa (17 anamorphs, 11 ascomycetes, 1 basidiomycete). *Acrogenospora sphaerocephala*, *Canalisporium* sp., *Dictyosporium heptasporum*, *Leptosphaeria ginimia*, *L. typharum*, *Massarina australiensis*, *Sporoschisma saccardoi*, and *Sporoschismopsis australiensis* were the most common taxa and were widely distributed on wood in streams of the Western Ghats. The bubble chamber incubation of bark and cambium revealed 30 aquatic hyphomycetes (bark, 28; cambium, 18). *Anguillospora longissima*, *Flagellospora curvula*, *F. penicillioides*, and *Lunulospora curvula* were most common in bark as well as cambium. There was only 1 species (*Helicomyces roseus*) that was identified following both incubation methods, indicating that methodology influences the detection of fungal communities. It is recommended that studies on freshwater fungi should incorporate both damp incubation and bubble chamber techniques.

Keywords Bark · Cambium · Diversity · Woody litter

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Introduction

Ingoldian fungi play an important role in the decomposition of allochthonous leaf litter in freshwater and constitute major intermediaries of energy flow in the food web (Bärlocher 1992). They produce mainly sigmoid and multiradiate conidia, which facilitate their dispersal and attachment on substrates in flowing waters (Ingold 1942; Webster and Descals 1981; Marvanová 1997; Gulis et al. 2007). These fungi employ "substrate capture" or ruderal strategy by production of asexual spores ($\sim$8/µg leaf dry mass = $\sim$1 M/leaf) as a consequence of the rapid nature of decomposing leaf litter in streams (Bärlocher 1992, 2009). More than 300 species of Ingoldian fungi are known throughout the world (Gulis et al. 2007), but only 34 taxa have been linked to teleomorphs of unrelated genera of mostly ascomycetes and a few basidiomycetes (Webster 1992; Marvanová 1997; Sivichai and Jones 2003). The presence of Ingoldian fungi on submerged wood, however, has rarely been reported as most studies have used damp chamber incubation techniques to reveal and identify the fungi present on the wood (Shearer 1992; Raja et al. 2007).

Ascomycetes and their anamorphs have also commonly been recorded on submerged wood (Shearer and Webster 1991; Pinruan et al. 2007; Raja et al. 2007). These lignicolous aquatic hyphomycetes, however, mostly differ from the Ingoldian fungi (also known as aquatic hyphomycetes) found on leaves, although there is some overlap. Most lignicolous aquatic hyphomycete genera have simple spores (e.g., *Acrogenospora*, globose; *Sporoschisma*, cylindrical) (Kodsueb et al. 2008) and rarely have multiradiate or sigmoid spores as found in the Ingoldian fungi on leaves (Marvanová 1997). Aquatic ascomycetes and their anamorphs mainly occur on woody debris and are valuable nutritional sources for invertebrates (Shearer 1993) because

of their enzymatic capabilities to degrade structural polysaccharides (Abdel-Raheem and Shearer 2002; Simonis et al. 2008). So far, about 500 species of ascomycetes have been reported from freshwater habitats (Shearer et al. 2007).

Studies carried out on freshwater fungi in India have mainly concentrated on the occurrence of Ingoldian fungi in water, foam, and leaf litter (Sridhar et al. 1992; Rajashekhar and Kaveriappa 2003). Ramesh and Vijaykumar (2006) have, however, studied freshwater ascomycetes on natural and baited woody litter in four streams of the Western Ghats.

The objective of the present study was to assess the occurrence and diversity of Ingoldian fungi and ascomycetes (including lignicolous hyphomycetes) on naturally submerged wood and bark in high-altitude streams of the Western Ghats, India. We employed damp chamber and bubble chamber incubation techniques. The bubble chamber technique has been used less often to study freshwater fungi on wood but can establish whether the Ingoldian fungi play any role in the decomposition of woody litter in streams (Shearer and Webster 1991). The damp chamber technique has usually been employed to study freshwater fungi on submerged wood and is used here for comparison with other studies.

Materials and methods

Streams

Naturally accumulated different varieties of woody litter amid rocks and boulders or fixed in soil or sediment were sampled from three sites of 12 high-altitude streams located in three mountain ranges of the Western Ghats: the Kudremukh range (Basrikallu, Lakya Dam, Yenne Halla, Vote Halli, and Sarpatheertha; 400–1190 m asl), the Agumbe range (Shivpura, Agumbe HP2, Agumbe Top, Agumbe HP14, and Nalur; 460–980 m asl), and the Madikeri range (Sampaje and Bagamandala; 510–560 m asl) during the southwest monsoon (August–September, 2006) (Table 1). The streams selected flow amid forest reserves consisting of semi-evergreen to evergreen riparian vegetation devoid of major human interferences. Temperature, pH, and conductivity of stream waters were assessed during sampling using a water analyzer (Systronics 371, Gujarat, India).

Wood samples

Wood samples were rinsed in freshwater in the laboratory to remove debris and processed within 24–48 h of sampling. Wood samples 1 cm in diameter were sorted out and a 15-cm section was cut from each sample for incubation. A composite sample of 50 wood pieces with intact bark was collected from each stream. Single pieces of wood were incubated separately (25 ± 2°C) on an autoclaved wet sand base in polythene bags for up to 6 months. They were screened once every 2–3 weeks using stereo- and compound microscopes for the occurrence of filamentous fungi.

Bark and cambium

Randomly selected bark was detached from the remaining wood samples and cut into pieces (0.5 × 3 cm), rinsed in freshwater, and incubated in bubble chambers in five replicates (five bark pieces per replicate) by suspending in 150 ml sterile distilled water in 250-ml Erlenmeyer flasks. Water in flasks was aerated through Pasteur pipettes using an aquarium pump for up to 48 h (23 ± 2°C). Aerated water was filtered through a Millipore filter (5 μm) and stained with aniline blue in lactophenol (0.1%). Stained filters were cut into half to mount on a microscope slide with lactic acid, and the conidia were identified (magnification, 200–1000×) and enumerated. The conidial output was expressed per gram dry mass of bark. The cambium of the wood were randomly selected and cut into pieces (0.3 × 0.5 × 3 cm) and processed as detailed for the bark samples.

Data analysis

The percent frequency of occurrence of each fungus on wood samples of each stream was determined:

$$\text{Frequency of occurrence}\,(\%) = \left[(\text{Number of wood pieces colonized}) \div (\text{Total wood pieces examined})\right] \times 100.$$

The mean percentage frequency of each fungus on wood and mean conidia produced by each fungus on bark/cambium was estimated:

$$\text{Mean}\,\%\,\text{frequency of occurrence/species} = (\text{Total}\,\%\,\text{frequency of fungi}) \div (\text{Total fungi on whole wood piece}).$$

Mean conidia/fungus/mg dry mass of bark or cambium = (Total conidia produced/mg dry mass of bark or cambium) ÷ (Total fungi recorded).

The Shannon diversity and evenness of fungi were estimated (Pielou 1975; Magurran 1988). To compare the fungal richness in each stream, the expected number of fungal species [$E_{(s)}$] in a random sample of n isolations taken from a total population of N isolations from wood samples was calculated by rarefaction index (Ludwig and Reynolds 1988). Percent Jaccard's index of similarity (JI)

Table 1 Details of 12 high-altitude Western Ghat streams sampled for woody litter (temperature, pH, and conductivity: $n = 3$, mean)

Stream (code), location, altitude, stream order, seasonal/perennial, and stream bottom	Sampling date	Temperature (°C)	pH	Conductivity (μS/cm)
Kudremukh range				
Basrikallu (BK), 13°29′37″N, 75°40′31″E, 880 m asl, second order, perennial, and rocky	September 7, 2006	25.0	6.9	40.9
Lakya Dam (LD), 13°13′29″N, 75°13′37″E, 840 m asl, second order, perennial, and rocky	September 7, 2006	22.5	6.8	27.6
Yenne Halla (YH),13°13′19″N, 75°07′05″E, 1190 m asl, third order, perennial, and rocky	September 7, 2006	22.5	6.9	26.2
Vote Halli (VH), 13°13′07″N, 75°18′21″E, 400 m asl, third order, perennial, rocky, and silt	September 7, 2006	22.5	6.8	39.7
Sarpatheertha (ST), 13°09′62″N, 75°18′29″E, 1190 m asl, second order, perennial, and rocky	September 7, 2006	23.0	6.6	29.9
Agumbe range				
Shivpura (SP), 13°26′00″N, 74°58′00″E, 460 m asl, fourth order, perennial, sandy, and silt	August 21, 2006	23.0	7.3	50.5
Agumbe HP2 (A1), 13°29′29″N, 74°04′14″E, 960 m asl, first order, seasonal, and rocky	August 21, 2006	22.0	7.2	30.5
Agumbe Top (A2), 13°29′47″N, 75°04′51″E, 980 m asl, first order, seasonal, and rocky	August 21, 2006	23.0	6.9	34.9
Agumbe HP14 (A3), 13°29′35″N, 75°04′28″E, 970 m asl, first order, seasonal, and rocky	August 21, 2006	22.0	7.4	55.7
Nalur (NL), 17°40′44″N, 75°13′05″E, 900 m asl, second order, seasonal, and silt	August 21, 2006	25.5	6.8	33.1
Madikeri range				
Sampaje (SPJ), 12°29′30″N, 75°35′25″E, 510 m asl, third order, perennial, and rocky	September 20, 2006	22.5	7.2	58.8
Bagamandala (BM), 12°23′10″N, 75°34′05″E, 560 m asl, third order, perennial, sandy, and silt	September 20, 2006	23.0	7.2	46.8
Mean ($n = 36$)		23.04	7.02	39.55
Range		22–25.5	6.6–7.4	26.2–58.8

was calculated pairwise among the streams based on the presence or absence of each fungus on whole wood, bark, and cambium (Kenkel and Booth 1992). To assess the difference in total species and conidial output of aquatic hyphomycetes between bark and cambium of 12 streams, a *t* test was employed (StatSoft Inc. 1995).

Results

The average stream water temperature, pH, and conductivity were 23.04°C, 7.02, and 39.55 μS/cm, respectively (Table 1). However, the streams of the Kudremukh range have a slightly more acid pH (6.6–6.9) with relatively low conductivity (26.2–40.9 μS/cm) than streams of the Agumbe and Madikeri ranges.

Fungi on wood samples in damp chambers

Damp incubation of submerged wood samples with bark yielded 29 taxa (17 anamorphs, 11 ascomycetes, and 1 basidiomycete) (Table 2). The total fungi at each site ranged between 7 (Lakya Dam and Shivpura) and 11 (Basrikallu, Agumbe HP2 and Sampaje) (Fig. 1a), whereas the mean frequency of occurrence per species ranged from 26% (Agumbe HP14) to 45% (Shivpura). Although the total number of species at Lakya Dam and Shivpura was lower (7), the mean frequency of occurrence per species was highest in Shivpura (45%), followed by Lakya Dam (44%) (Fig. 1b). The most common taxon was *Sporoschismopsis australiensis* (41%), followed by *Acrogenospora sphaerocephala* (40%), *Leptosphaeria typharum* (32%), *Sporoschisma saccardoi* (32%), *Massarina australiensis* (32%), *Canalisporium* sp. (28%), *Leptosphaeria ginimia* (22%), and *Dictyosporium heptasporum* (21%). These fungi were common and distributed in at least five streams and up to a maximum of ten streams. The diversity was highest in Basrikallu and lowest in Lakya Dam, which coincided with observed species richness. The rarefaction curves extended beyond 100 wood samples in Sarpatheertha, Basrikallu, and Sampaje streams (Fig. 2).

Table 2 Frequency of occurrence (%), species richness, and diversity of fungi on whole woody litter collected from 12 high-altitude Western Ghat streams

Fungus	Streams												MFOS
	Kudremukh range					Agumbe range					Madikeri range		
	BK	LD	YH	VH	ST	SP	A1	A2	A3	NL	SPJ	BM	
Mitosporic fungi													
Acrogenospora sphaerocephala (Berk. & Broome) M.B. Ellis	62.9	61.1	62.9	50.0	44.4	66.7	46.7	53.3	26.7	–	–	–	39.6
Cacumisporium capitulatum (Corda) S. Hughes	05.7	–	–	–	–	–	–	–	–	–	–	–	00.5
Canalisporium caribense (Hol.-Jech. & Mercado) Nawawi & Kuthub.	–	–	–	–	–	–	–	–	–	–	58.8	56.1	09.6
Canalisporium sp.	54.3	55.6	–	62.5	37.7	–	53.3	13.3	–	–	55.9	–	27.7
Chloridium reniforme Matsush.	–	–	05.7	–	–	–	–	–	–	–	02.9	–	00.7
Codinea sp.	–	–	–	–	–	–	–	–	06.7	–	–	–	00.6
Dictyosporium heptasporum (Garov.) Damon	57.1	55.6	45.7	41.7	53.3	–	–	–	–	–	–	–	21.1
Endophragmia cesatii (Mont.) M.B. Ellis	–	–	–	–	–	53.3	–	–	–	33.3	–	–	07.2
Exserticlava triseptata (Matsush.) S. Hughes	–	–	–	–	–	–	20.0	13.3	40.0	–	–	–	06.1
Gliocladium viride Matr.	08.6	–	–	–	–	–	–	–	–	–	–	–	00.7
Helicomyces roseus Link[a]	17.1	11.1	–	–	–	–	–	–	–	–	–	04.9	02.8
Phoma apiicola Kleb.	–	–	11.4	–	–	–	–	–	–	–	–	–	0.95
Pleurothecium recurvatum (Morgan) Höhn.	–	–	–	–	–	–	06.7	–	–	–	–	–	00.6
Spegazzinia intermedia M.B. Ellis	22.9	–	–	–	–	–	–	–	–	40.0	11.8	14.6	07.4
Sporoschisma saccardoi E.W. Mason & S. Hughes	45.7	–	57.1	58.3	53.3	60.0	53.3	33.3	26.7	–	50.0	53.7	31.7
Sporoschismopsis australiensis Goh & K.D. Hyde	–	–	60.0	–	40.0	26.7	60.0	53.3	53.3	53.3	–	34.1	41.0
Veronaea caricis M.B. Ellis	–	–	–	–	–	–	–	–	13.3	–	14.7	–	02.3
Ascomycetes													
Aniptodera lignatilis K.D. Hyde	–	–	–	–	–	–	–	40.0	26.7	06.7	–	–	06.1
Boerlagiomyces sp.	–	–	–	–	–	33.3	–	–	–	–	55.9	–	07.4
Eutypa acharii Tul. & C. Tul.	–	–	–	–	–	–	–	–	–	–	–	12.2	01.0
Leptosphaeria ginimia K.M. Tsui, K.D. Hyde & Hodgkiss	40.0	58.3	37.1	–	35.6	–	26.7	–	–	33.3	–	36.6	22.3
L. typharum (Desm.) P. Karst.	42.9	50.0	37.1	41.7	42.2	–	40.0	–	–	46.7	58.8	21.9	31.8
Lophiostoma frondisubmersum (K.D. Hyde) E.C.Y. Liew, Aptroot & K.D. Hyde	–	–	–	–	–	–	–	–	13.3	–	–	–	01.1
Massarina australiensis K.D. Hyde	60.0	–	–	41.7	31.1	40.0	40.0	46.7	26.7	40.0	41.2	12.2	31.6
Nectria byssicola Berk. & Broome	–	–	–	–	–	–	13.3	–	–	–	14.7	–	02.3
Phyllachora sylvatica Sacc. & Speg.	–	13.9	–	16.7	–	–	–	–	–	33.3	–	–	05.3
Torrentispora fibrosa K.D. Hyde, Wai H. Ho, E.B.G. Jones, K.M. Tsui & S.W. Wong	–	–	14.3	–	–	33.3	–	20.0	–	–	02.9	–	05.9
Zopfiella latipes (N. Lundq.) Malloch & Cain	–	–	–	–	–	–	06.7	–	–	–	–	–	00.6
Basidiomycete													
Unidentified species	–	–	–	04.2	–	–	–	–	–	–	–	–	00.4
Total species	11	07	09	08	08	07	11	08	09	08	11	09	

Table 2 continued

Fungus	Streams												MFOS
	Kudremukh range					Agumbe range					Madikeri range		
	BK	LD	YH	VH	ST	SP	A1	A2	A3	NL	SPJ	BM	
Expected number of species [$E_{(s)}$] out of 40 random wood samples	25	26	25	21	28	15	15	15	14	15	14	27	
Cumulative species	11	12	16	17	17	19	23	24	27	27	28	29	
Mean percent frequency of occurrence/species	37.9	43.7	36.8	39.6	42.2	44.8	33.3	34.2	25.9	35.8	33.4	27.4	
Shannon diversity	3.220	2.619	2.904	2.793	2.978	2.736	3.201	2.832	2.972	2.880	3.059	2.863	
Shannon evenness	0.931	0.933	0.916	0.931	0.993	0.975	0.925	0.944	0.938	0.960	0.884	0.903	

Kudremukh range: BK, Basrikallu; LD, Lakya Dam; YH, Yenne Halla; VH, Vote Halli; ST, Sarpatheertha

Agumbe range: SP, Shivpura; A1, Agumbe HP2; A2, Agumbe top; A3, Agumbe HP14; NL, Nalur

Madikeri range: SPJ, Sampaje; BM, Bagamandala

MFOS, mean % frequency of occurrence/stream

[a] Common in bark and rare in cambium; see Table 3)

Fungi on bark and cambium in bubble chambers

Aeration of bark and cambium yielded 30 taxa of Ingoldian fungi (bark, 28; cambium, 18), with 16 taxa that colonized both substrates (Table 3). The total taxa from each site ranged from 5 (Bagamandala, Lakya Dam, and Yenne Halla) to 13 (Sampaje) in bark, and from 3 (Basrikallu) to 10 (Shivpura) in cambium (Fig. 3). The total conidia/g dry mass of bark ranged between 50 (Agumbe Top) and 1,137 (Shivpura), and that in cambium from 318 (Nalur) to 16,370 (Vote Halli) (Fig. 4a). The cumulative species was higher in bark than in cambium (Table 3). However, generally conidial output from the cambium is higher than from bark, indicating the ability of Ingoldian fungi to colonize the cambium by penetrating through the bark.

The most common fungus in bark was *Flagellospora curvula* (mean, 85 conidia/g dry weight/stream), followed by *Helicomyces roseus* (83), *Anguillospora longissima* (74), *A. crassa* (34), *Lunulospora curvula* (32), and *Flagellospora penicillioides* (20). In cambium, *Lunulospora cymbiformis* was the most commonly occurring fungus (mean, 2737 conidia/g dry mass/stream), followed by *Anguillospora longissima* (1167), *Lunulospora curvula* (949), *Triscelophorus acuminatus* (895), *Flagellospora curvula* (227), *Triscelophorus konajensis* (177), *Arborispora dolichovirga* (100), *Flagellospora penicillioides* (62), *Tetracladium marchalianum* (23), and *Flabellospora verticillata* (13). The diversity on bark was highest in Sarpatheertha and lowest in Agumbe HP14 (Table 3); the diversity for cambium was highest at Nalur and lowest for Sampaje. The *t* test between species richness in bark and in cambium showed a significant difference ($P = 0.025$); conidial output was also significant ($P = 0.0004$).

Similarity index

Of 66 pairwise comparisons of occurrence, only 8 pairs ranged between 50% and 67% in wood samples (w); in the remaining, it was 7% and 46%, which reveals more dissimilarity between fungal communities in wood (Table 4). Surprisingly, the similarity of aquatic hyphomycetes in bark + cambium (bc) ranged between 56% and 77% (except for 1 pair at 44%), indicating more similarity in aquatic hyphomycete communities on bark and cambium in the streams of Western Ghats.

Discussion

The most interesting finding in this study is that the fungi revealed from bubble chamber incubation differed widely from those identified from damp chamber incubation. The fungi from bark and cambium placed in the bubble chamber were typical Ingoldian fungi with multiradiate or sigmoid spores (Marvanová 1997), whereas those from damp chamber incubation of wood were ascomycetes, a basidiomycete, or typical lignicolous hyphomycetes (Tsui et al. 2003; Raja et al. 2007; Kodsueb et al. 2008).

Comparison of lignicolous fungi with other studies

Among 17 lignicolous anamorphic taxa found on woody litter, *Acrogenospora sphaerocephala*, *Canalisporium* sp., *Dictyosporium heptasporum*, *Sporoschisma saccardoi*, and *Sporoschismopsis australiensis* were most frequent (21–41%/stream). Some anamorphic taxa found in our study were common to other tropical, subtropical, and

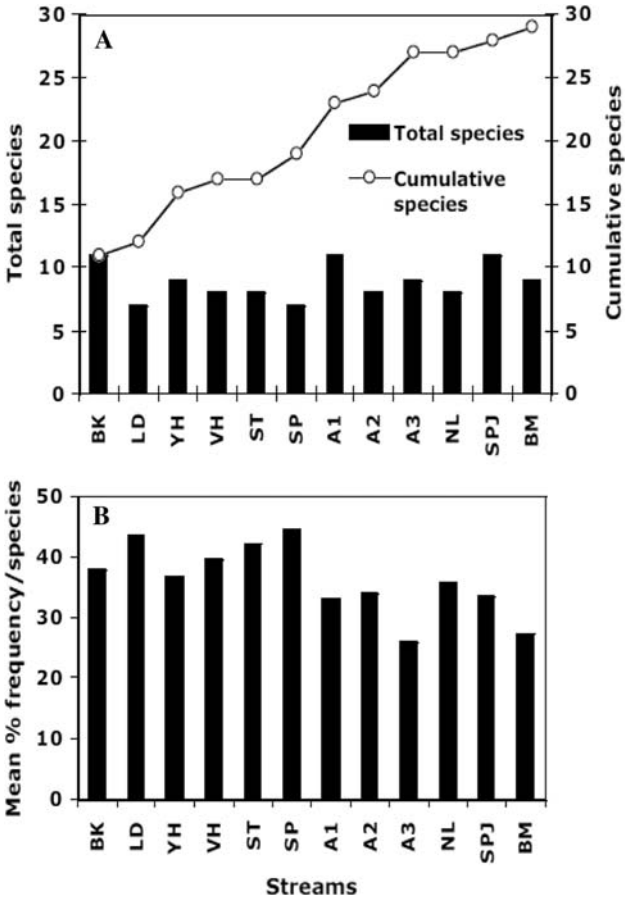

Fig. 1 Total species, cumulative species (**a**), and mean percent frequency/species (**b**) of fungi on woody litter of 12 high-altitude streams of Western Ghats using damp chamber incubation (see Table 1 for details of location)

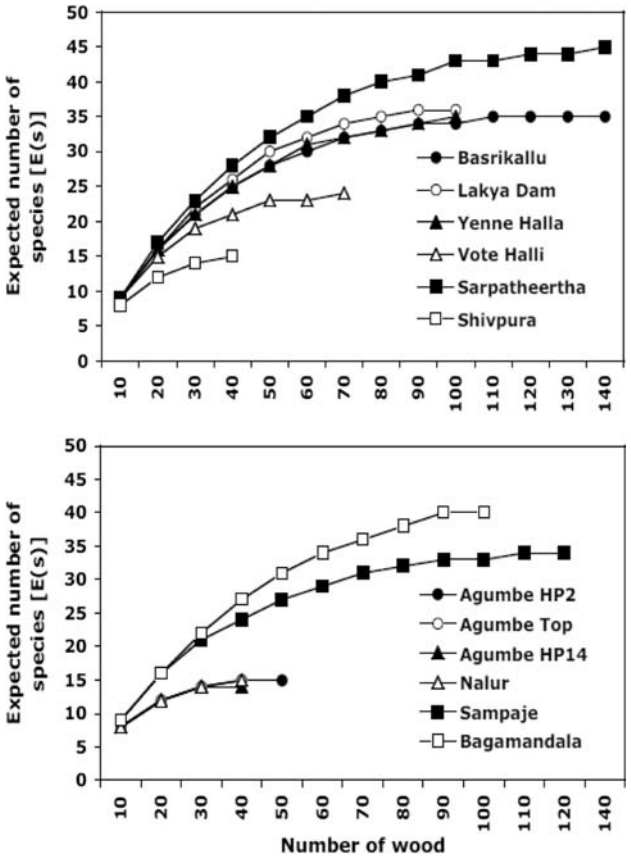

Fig. 2 Rarefaction curve of fungi on woody litter of 12 high-altitude streams of Western Ghats using damp chamber incubation: number of wood samples versus expected number of species [$E_{(s)}$]

temperate terrestrial and aquatic habitats: *Acrogenospora sphaerocephala* (Hong Kong and Thailand: Sivichai et al. 2000; Tsui and Hyde 2004), *Canalisporium caribense* (Brunei and Thailand: Hyde and Goh 1998; Sivichai et al. 2000; Ho et al. 2001), *Helicomyces roseus* (Brunei, Hong Kong, Thailand, and North Queensland: Hyde and Goh 1997; Sivichai et al. 2000, 2002; Ho et al. 2001, 2002), *Pleurothecium recurvatum* (Brunei: Ho et al. 2001), and *Sporoschisma saccardoi* (Brunei, Hong Kong and Thailand: Sivichai et al. 2000; Ho et al. 2001, 2002).

Shearer (2001) listed six lignicolous ascomycetes having a wide distribution (*Aniptodera chesapeakensis*, *A. lignatilis*, *Annulatascus velatisporus*, *Halosarpheia retorquens*, *Massarina ingoldiana*, and *Nais inornata*). Among them, *A. lignatilis* was found in our study (6.1%), Hong Kong (Tsui and Hyde 2004), and St. Marie-Louis River in the Seychelles (Hyde and Goh 1998). The remaining ascomycetes found in our study have been recorded from other tropical regions (*Leptosphaeria ginimia*, Hong Kong; *Nectria byssicola*, Hong Kong, Brunei, and Malaysia; *Torrentispora fibrosa*, Hong Kong and Brunei; *Lophiostoma frondisubmersum*, Brunei) (Hyde et al. 2000; Ho et al. 2001; Tsui et al. 2001; Fryar et al. 2004; Tsui and Hyde 2004). To our knowledge, there has been only one study on lignicolous fungi in streams from the Western Ghats, with a report of 14 ascomycetes (Ramesh and Vijaykumar 2006). With the exception of *Zopfiella latipes*, none were common in our study. Lignicolous fungi reported from water-cooling towers of Madras (southeast coast, India) were also not found in our study (Udaiyan 1989; Udaiyan and Hosagoudar 1991). Among the most frequent lignicolous fungal genera in the tropics (Australia, Brunei, Ecuador, Malaysia, and Philippines), only *Aniptodera*, *Boerlagiomyces*, and *Massarina* are common to our study (Hyde et al. 1997). Because up to 70% of freshwater ascomycetes have been reported only once from freshwater streams, this has resulted in difficulty in understanding their global distribution and endemism (Shearer et al. 2007, 2008).

The diversity and species richness of lignicolous fungi in our study was highest in Basrikallu stream and least in Lakya Dam. Heavy metals from the Kudremukh iron ore mine might have impoverished the lignicolous fungi in Lakya Dam. An earlier study at Sitabhumi River near the

Table 3 Aquatic hyphomycetes (conidia/g dry mass) on bark and cambium (in parentheses), species richness, and diversity in 12 high-altitude Western Ghat streams

Fungus	Kudremukh range					Agumbe range					Madikeri range		MCGS	Reports
	BK	LD	YH	VH	ST	SP	A1	A2	A3	NL	SPJ	BM		
Alatospora acuminata Ingold				11				2					1.1	2,6,7,8,13,14, 15,16,17,21
Anguillospora crassa Ingold	33	75	75 (82)	58			28	19	11	37	12	65	34.4 (6.8)	2,7,8,9,13,15,16,
A. longissima (Sacc. & P. Syd.) Ingold	95	22 (3234)	217 (295)	255 (4307)	52 (133)	90 (1109)	29 (250)	4 (220)	75	10 (7)	12 (2118)	27 (2326)	74 (1167)	1,2,7,8,9,13,16, 17,20,22
Arborispora dolichovirga K. Ando				11		(96)		(441)	(155)			(511)	0.9 (100)	
Campylospora chaetocladia Ranzoni	4				3								0.6	7,8,12,21
C. filicladia Nawawi	7										20		2.3	10
C. parvula Kuzuha	4										60		5.3	
Cancellidium applanatum Tubaki						7 (33)							0.6 (2.8)	
Clavariopsis aquatica De Wild.											3		0.3	2,6,7,8,13,15, 16,20,21,22
Cylindrocarpon sp.		(63)											(5.3)	
Flabellospora crassa Alas.										(4)	9		0.8 (0.3)	
F. verticillata Alas.										(21)	33 (131)		2.8 (12.7)	
Flagellospora curvula Ingold	131	74 (479)	27 (160)	11 (533)	15 (1211)	599 (260)		10	8	28 (84)	43	70	84.7 (227)	2,14,16,22
F. penicillioides Ingold	67	9 (168)				17	31			46	23 (574)	52	20.4 (61.8)	14,21
Heliscella stellata (Ingold & V.J. Cox) Marvanová	4		4										0.7	13,22
Helicomyces roseus Link[a]	8				9	237 (60)	21	13	510		193		82.6 (5.0)	3,4,5,18
Helicosporium sp.					3				11	3			1.4	
Isthmotricladia gombakiensis Nawawi					12								1.0	
Lunulospora curvula Ingold	40 (505)	12 (988)	13 (1580)	28 (2497)	33 (1209)	144 (1367)	2 (677)		29 (1367)	82 (64)	(1134)		31.9 (949)	15,16,20,21
L. cymbiformis K. Miura	(876)	(3996)	(2830)	56 (8533)	(1585)		(1518)		(3335)	(18)	(9100)	(1055)	4.7 (2737)	21
Nawawia filiformis (Nawawi) Marvanová					3								0.3	4,19

Table 3 continued

Fungus	Kudremukh range					Agumbe range					Madikeri range		MCGS	Reports
	BK	LD	YH	VH	ST	SP	A1	A2	A3	NL	SPJ	BM		
Phalangispora constricta Nawawi & J. Webster						(27)							(2.3)	
Tetracladium marchalianum De Wild.	5							(281)					0.4 (23.4)	2,13,14,15,17, 22
Tricladium fuscum Nawawi	5		(53)			15				2			1.8 (4.4)	
Tripospermum myrti (Lind) S. Hughes					15								1.3	
Triscelophorus acuminatus Nawawi	(330)		22	22 (500)	6 (242)	14 (2548)	6 (1586)	(2067)	(2991)	(83)	3	(389)	6.1 (895)	11,21
T. konajensis K.R. Sridhar & Kaver.						14 (483)	(220)	(1173)		2 (37)	3	(205)	1.6 (177)	
T. monosporus Ingold						(53)		2				5	0.6 (4.4)	16,17
Varicosporium elodeae W. Kegel											20		1.7	14,22
Unidentified sp. (tetraradiate spore)					3								0.3	
Total species	12 (3)	5 (6)	5 (6)	8 (5)	11 (5)	9 (10)	6 (5)	6 (5)	6 (4)	8 (8)	13 (5)	5 (5)		
Cumulative species	12 (3)	12 (7)	12 (9)	14 (9)	19 (9)	21 (15)	21 (15)	22 (16)	22 (16)	22 (18)	26 (19)	26 (19)		
Total conidia/g dry mass	403 (1711)	192 (8928)	359 (5000)	452 (16370)	154 (4380)	1137 (6036)	117 (4251)	50 (4182)	644 (7848)	210 (318)	434 (13127)	219 (4486)		
Shannon diversity	2.644 (1.472)	1.875 (1.786)	1.685 (1.557)	2.071 (1.725)	2.811 (1.940)	2.000 (2.244)	2.265 (1.945)	2.163 (1.844)	1.108 (1.606)	2.263 (2.534)	2.712 (1.360)	2.712 (1.360)	2.035 (1.849)	
Shannon evenness	0.738 (0.929)	0.808 (0.691)	0.652 (0.602)	0.690 (0.743)	0.813 (0.836)	0.631 (0.675)	0.876 (0.838)	0.827 (0.794)	0.729 (0.803)	0.754 (0.845)	0.733 (0.586)	0.733 (0.586)	0.877 (0.796)	

Kudremukh range: BK, Basrikallu; LD, Lakya Dam; YH, Yenne Halla; VH, Vote Halli; ST, Sarpatheertha

Agumbe range: SP, Shivpura; A1, Agumbe HP2; A2, Agumbe Top; A3, Agumbe HP14; NL, Nalur

Madikeri range: SPJ, Sampaje; BM, Bagamandala

MCGS mean conidia/g dry mass/stream

Reports: 1, Eaton and Jones 1971; 2, Gönczöl and Révay 2003; 3, Ho et al. 2001; 4, Ho et al. 2002; 5, Hyde and Goh 1997; 6, Jones and Oliver 1964; 7, Kane 1980; 8, Kane et al. 2002; 9, Lamore and Goos 1978; 10, Nawawi 1974; 11, Nawawi 1975; 12, Nilsson 1964; 13, Révay and Gönczöl 1990; 14, Sanders and Anderson 1979; 15, Shearer 1992; 16, Shearer and Webster 1991; 17, Shearer and von Bodman 1983; 18, Sivichai et al. 2000; 19, Sivichai et al. 2002; 20, Sládečková 1963; 21, Thomas et al. 1992; 22, Willoughby and Archer 1973

[a] Rare in whole wood on damp incubation, see Table 2

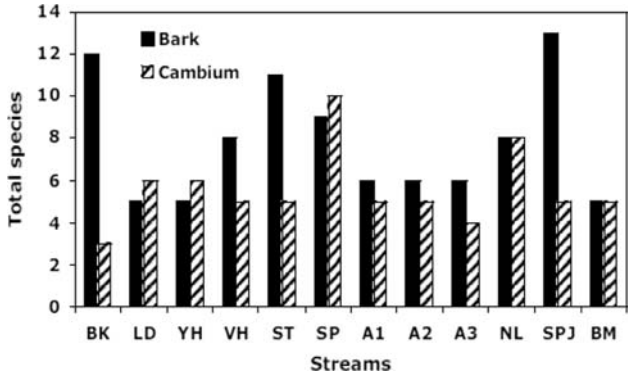

Fig. 3 Total species of fungi in bark and cambium of woody litter of 12 high-altitude streams of Western Ghats using bubble chamber incubation (see Table 1 for details and abbreviations of locations)

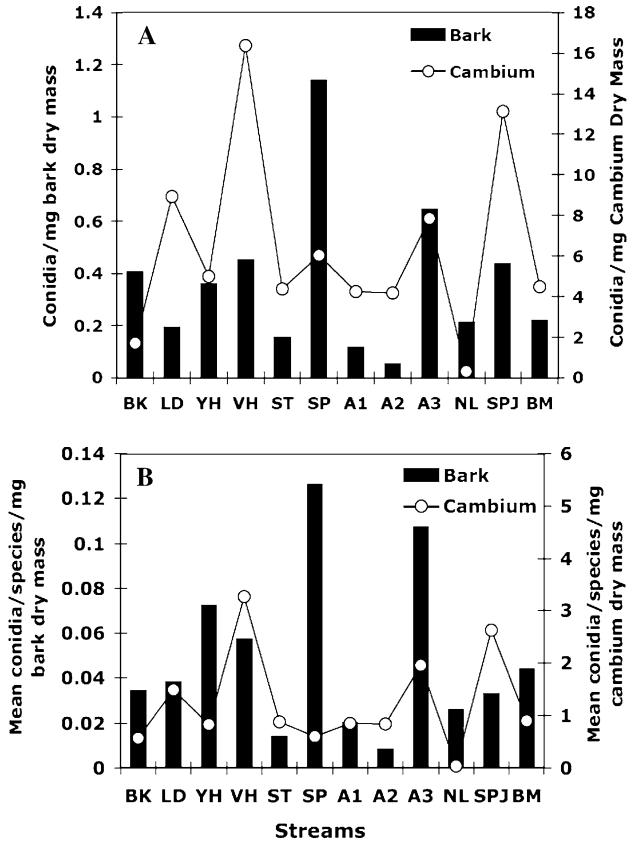

Fig. 4 Conidia of aquatic hyphomycetes/mg dry mass of bark and cambium (**a**) and mean conidia/species/mg dry mass of bark and cambium (**b**) of woody litter of 12 high-altitude streams of Western Ghats using bubble chamber incubation (see Table 1 for details of locations)

Kudremukh iron ore mine also showed low fungal occurrence on leaf litter (Raghu et al. 2001). Lignicolous fungi were more dissimilar among the streams of Western Ghats, supporting the view of occurrence of diverse mycota.

Table 4 Jaccard's percent similarity of fungal species in whole wood (w) and bark + cambium (bc) of 12 high-altitude Western Ghat streams

		Kudremukh range				Agumbe range					Madikeri range	
		LD	YH	VH	ST	SP	A1	A2	A3	NL	SPJ	BM
BK	w	50	31	50	58	20	60	29	13	21	29	42
	bc	65	68	62	62	63	65	60	67	63	69	61
LD	w	36	42	44	08	29	17	07	25	20	14	
	bc	67	67	58	56	67	56	65	65	62	65	
YH	w	39	50	33	33	31	25	15	23	29		
	bc	71	60	63	69	61	67	68	61	63		
VH	w	67	27	46	40	25	31	29	23			
	bc	60	60	65	67	77	64	59	69			
ST	w	36	64	46	27	20	31	42				
	bc	59	60	58	67	59	44	57				
SP	w	29	42	36	18	29	25					
	bc	67	65	64	63	61	67					
A1	w	46	31	27	27	33						
	bc	65	73	68	68	69						
A2	w	67	23	31	21							
	bc	65	61	59	71							
A3	w	21	20	18								
	bc	67	63	67								
NL	w	20	42									
	bc	71	67									
SPJ	w	33										
	bc	65										

Kudremukh range: BK, Basrikallu; LD, Lakya Dam; YH, Yenne Halla; VH, Vote Halli; ST, Sarpatheertha

Agumbe range: SP, Shivpura; A1, Agumbe HP2; A2, Agumbe top; A3, Agumbe HP14; NL, Nalur

Madikeri range: SPJ, Sampaje; BM, Bagamandala

Comparison of Ingoldian fungi with other studies

Woody litter consisting of Ingoldian fungi may serve as a reservoir to colonize detritus in freshwater streams. However, so far Ingoldian fungi in submerged wood in freshwater have been poorly investigated (Tsui et al. 2003). Among the Ingoldian fungi found in our study, many are also inhabitants of temperate streams. Based on the literature, Shearer (1992) listed 46 Ingoldian fungi on woody litter in temperate and tropical freshwaters (see also Table 3). It is interesting that *L. cymbiformis* was the most dominant fungus on bark and twigs of *Eucalyptus* as seen in cambium in our study (see Table 3).

In damp incubation, in addition to non-Ingoldian fungi, *Nawawia filiformis* was recovered from the submerged wood in streams of Hong Kong and Thailand (Sivichai et al. 2002; Ho et al. 2002), as was *Helicomyces roseus* in damp and bubble chamber incubation in our study. Damp incubation of leaf and woody litter sampled from a coastal stream also yielded conidia of *Triscelophorus konajensis* (K.R. Sridhar, personal observation). Based on previous reports, among the Ingoldian fungi found in our study, *Alatospora acuminata*, *Anguillospora crassa*, *A. longissima*, *Clavariopsis aquatica*, and *Tetracladium marchalianum* dominate woody litter (see Table 3). However, their distribution and conidial output were sparse except for *A. crassa* and *A. longissima*. *Flagellospora curvula*, *Lunulospora curvula*, *L. cymbiformis*, and *Triscelophorus acuminatus* were widely distributed and produced many conidia. Shearer (1992) has listed the most predominant species of Ingoldian fungi on submerged wood based on frequency of occurrence. Some fungi found in our study also coincide with that observation (e.g., *Alatospora acuminata*, *Anguillospora longissima*, and *Clavariopsis aquatica*). Interestingly, frequent or abundant Ingoldian fungi on woody litter showed considerable exoenzymatic capabilities (e.g., *Alatospora acuminata*, *Anguillospora crassa*, *A. longissima*, *Clavariopsis aquatica*, and *Tetracladium marchalianum*) (Shearer 1992).

The Ingoldian fungi in bark and cambium of woody litter among the streams of Western Ghats showed high similarity (56–77%). However, the species richness as well as conidial output in bark ($P = 0.025$) and in cambium ($P = 0.0004$) differed significantly. Ingoldian fungi on the leaf litter of rivers of Western Ghats also showed similar trends (Maddodi et al. 2009). The mean number of conidia produced by the Ingoldian fungi from a river in Devon, England was greater than 700,000/48 h/twig by bubble chamber incubation (Shearer and Webster 1991). However, the conidial output from bark and cambium of woody litter in the Western Ghats was lower compared to the River Devon (50–1,137/g vs. 318–16,370/g) (see Table 3; Fig. 4). Higher conidial output in cambium than bark indicated the ability of Ingoldian fungi to colonize the cambium by penetrating the bark. However, those species showed very low conidial output from the bark, leading us to suspect that they have been trapped by bark. It is also possible that some inhibitory substances in bark (e.g., suberin) might be responsible for low conidial production from bark. The total fungi (Basrikallu, Sarpatheertha, and Sampaje) and conidial biomass (Sarpatheertha and Agumbe HP 14) in bark in some streams are higher than other streams (see Fig. 4). Sarpatheertha stream has the highest diversity of Ingoldian fungi in bark. Raviraja et al. (1998) predicted that the water chemistry influences the number of fungal species and their composition in leaf litter of streams of the Western Ghats. They indicated that the greatest variability in species richness in streams was due to contrasting pH (6.8–7.2). In the current study, except for two streams (pH 7.3, 7.4), the pH was ranged between 6.8 and 7.2, which supports this hypothesis.

Differences in species composition and their assessment

With the exception of *Helicomyces roseus*, there was no overlap of anamorphic fungal taxa identified in either incubation method. More or less equal numbers of lignicolous and Ingoldian fungi have been recovered by these techniques (29 vs. 30). However, the quantity of wood material used in the two techniques varied drastically. Similarly, more time was needed to assess lignicolous fungi than Ingoldian fungi. It is difficult to assess all the fungi present in a substrate without employing different qualitative and quantitative techniques. A single technique will underestimate the total fungal composition in a substratum or may be biased toward a specific fungal group. Woody litter will be usually damp incubated to assess the colonizing fungi. It is difficult assess the abundance and diversity of patchy distributed ascomycetes on wood (Shearer et al. 2004). For a fair assessment of ascomycetes, sampling the naturally submerged and baited substrata in different gradients (e.g., riffles, pools, semiterrestrial) and seasons in freshwater should be carried out (Shearer et al. 2004). In addition, immersing different types of wood during different seasons is necessary to connect the pattern of fungal colonization to wood quality and water chemistry.

Roles of lignicolous versus Ingoldian fungi and future studies

Substantial fungal colonization on woody litter of high-altitude streams of the Western Ghats indicates their importance in wood decomposition. However, many questions remain unanswered, and careful experiments

should be designed to test various hypothesis. Are Ingoldian fungi superficial colonizers of wood or are they involved in wood decomposition through their perfect states? Are lignicolous fungi and Ingoldian fungi competing for resources? Are there any differences in the role of lignicolous fungi versus Ingoldian fungi in wood decomposition? Does human interference in freshwater ecosystems affect these fungal groups differentially?

We only used bark and cambium in the bubble chamber incubation technique as we suspected that the Ingoldian fungi were early superficial colonizers. In future studies, it would be interesting to take wood samples incubated in a damp chamber and subject them to the bubble chamber technique to establish whether the Ingoldian fungi have died out. K.D. Hyde has observed Ingoldian fungi on recently collected (within 24 h) wood samples but not on older incubated samples (unpublished data). This observation may indicate that Ingoldian fungi grow on submerged wood but do not have the ability to survive (or at least reproduce) out of the water. More interesting results may emerge by sampling selected streams over one or more seasonal cycles with water filtration to connect Ingoldian fungal populations in water with those in wood. It would also be possible to extract and analyze whole DNA from freshly removed and damp chamber-incubated wood samples to establish which fungi are present (Duong et al. 2006; Bärlocher 2007; Hyde and Soytong 2008; Seena et al. 2008).

Acknowledgments One of the authors (K.S.K.) acknowledges the award of a junior research fellowship under SC/ST Cell, Mangalore University, and the Rajeev Gandhi Fellowship, University Grants Commission, New Delhi. We thank B.S. Kadamannaya, Department of Zoology, FMKMC Mangalore University College, Madikeri, for field assistance.

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