Are there any substrate preferences in aquatic hyphomycetes?

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Aquatic hyphomycete assemblages on different types of plant litter in Belarus rivers and streams were investigated to determine whether any substrate specificity or preferences were apparent. Pooled samples (146) from 92 watercourses were analysed. Colonization coefficients were computed for each fungal taxa and substrate type and the resulting matrix analysed with principal component analysis and cluster analysis. The results demonstrate that some substrates support relatively specific aquatic hyphomycete assemblages and it is possible to ordinate plant litter types by means of their fungal complexes. This suggests selective colonization by fungi, i.e. substrate preferences at least in some species. Wood and grass blades bear fungal assemblages clearly distinct from those supported by tree leaf litter (with higher percentage of scolecosporous and antagonistic species). Ordination of plant litter types could be explained by size of substrate units, their chemical composition (in particular lignin content) and, consequently, breakdown rate that affects fungal colonization.

INTRODUCTION

Leaves and twigs of riparian trees and shrubs and to lesser extent grass blades represent major substrates for aquatic hyphomycetes in forest streams. Conifer needles are less intensively colonized due to the presence of thick waxy cuticles and phenolics (Bärlocher & Oertli 1978a, b, Michaelides & Kendrick 1978). Macrophytes, if present, also support species-poor aquatic hyphomycete assemblages (Kirby, Webster & Baker 1990).

It is generally thought that there are no obvious substrate preferences in aquatic hyphomycetes, i.e. most species are capable of colonizing a wide range of substrates (Webster & Descals 1981, Bärlocher 1992, Suberkropp 1992). Differences in dominance patterns and frequencies on different types of leaf litter, however, have been observed (Bärlocher & Kendrick 1974, Suberkropp & Klug 1976, Chamier & Dixon 1982, Shearer & Lane 1983). Bärlocher (1992) suggested that most aquatic hyphomycetes (at least those occurring on leaf litter) exploit a ruderal strategy, i.e. rapid colonization of available resources and production of propagules. Such a strategy could mask substrate preferences.

Nevertheless, it seems that some substrate preferences do occur. In some studies, species composition of conidia in stream water demonstrate little to moderate similarity with fungal species on leaf litter or wood (Sanders & Anderson 1979, Chamier & Dixon 1982, Shearer & Lane 1983) indicating selective colonization. However, when more accurate comparison based on composition of conidia in stream water and distribution of conidia released during the breakdown of the substrate has been done the percentage similarity reached up to 66.8 % (Bärlocher 1982). The idea of substrate selectivity by some aquatic hyphomycetes is supported by observations that changes in species composition, frequency of occurrence or conidia concentration in water occur in response to differences in riparian vegetation (Gönczöl 1975, Bärlocher 1982, Thomas, Chilvers & Norris 1991, Gönczöl, Révay & Csontos 1999). Colonization by aquatic hyphomycetes starts with the attachment of conidia to a substrate surface and is affected by its physical characteristics (surface energy, hardness, and specific topographical stimuli (Harrison, Moss & Jones 1988, Read, Moss & Jones 1992) – characteristics that have hardly ever been determined for leaves). Colonization also depends on the size and shape of the substrate unit and, consequently, differences in water flow in the immediate vicinity, the chemical composition of the substrate (certain substances will stimulate or inhibit germination) and features inherent to fungal species (conidial configuration and size which affect trapping, rate and percentage of germination). Initial differences in colonization will be modified by enzymatic capabilities and by interactions between fungi and with bacteria and invertebrates. A number of external factors such as stream temperature and availability of dissolved nutrients complicate matters further.

The aim of this study was to compare aquatic hyphomycete

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Table 1. Aquatic hyphomycetes on common substrates in Belarus watercourses, colonization coefficients (CC) and frequencies of occurrence on substrates in pooled samples (FOS).

Aquatic hyphomycete	Colonization coefficient								Mean CC	FOS
	AL	B	P	Q	S	T	G	W		
Actinosporella megalospora	1.00	0	1.00	1.00	0	–	–	–	0.6	0.01
Alatospora acuminata aggr.	0.86	0.67	0.67	0.5	0.7	0.71	0.39	0.25	0.59	0.59
A. pulchella	1.00	–	–	–	1.00	–	1.00	0.5	0.88	0.01
Anguillospora crassa	0.25	0	–	–	0	–	0.2	0.4	0.17	0.01
A. longissima	0.93	0.5	0.84	0.53	0.81	0.67	0.66	0.64	0.7	0.76
A. rubescens	0	–	–	–	0	–	1.00	0	0.25	0.01
Anguillospora sp.	–	–	–	0	–	–	–	1.00	0.5	0.01
Articulospora atra	0	0	–	0	0	–	0	0	0#	0.01
A. tetracladia	0.78	0.5	1.00	1.00	0	0.5	0.14	0	0.49	0.05
Camposporium pellucidum	0.5	0	0	0	0	–	0	0.5	0.14	0.02
Clavariopsis aquatica	0.89	0.33	0.33	0.5	0.65	0.6	0.16	0.26	0.47	0.36
Clavatospora longibrachiata	0.71	0	1.00	0.33	0.25	–	0.33	0.32	0.42	0.19
Dimorphospora foliicola	–	–	0	–	0	–	–	1.00	0.33	0.01
Filosporella annelidica	–	–	–	–	–	–	–	1.00	1.00	0.01
F. exilis	0	0	–	–	0	–	0.75	0.5	0.25	0.03
F. versimorpha	0	0	–	–	–	0	1.00	0	0.2	0.03
Flagellospora curvula	0.76	0.5	0.5	0.5	0.68	0	0.1	0.12	0.4	0.27
Fusarium cavispermum	0	–	0.5	0	0.2	–	0	0.83	0.26	0.08
Heliscella stellata	0.14	0	–	0	0	0	0	0.14	0.04	0.06
Heliscus lugdunensis	0.74	0	0.4	0.33	0.29	1	0	0.35	0.39	0.16
Lateriramulosa uni-inflata	–	0	0	0	0	0	0	0	0#	0.01
Lemonniera cfr alabamensis	1.0	–	0	–	0.5	–	–	–	0.5	0.02
L. aquatica	0.93	1.00	0.5	0.67	0.73	0.86	0.17	0	0.61	0.33
L. filiformis	1.00	1.00	–	–	0.5	–	0.4	0.33	0.65	0.03
L. terrestris	0.8	0	1.00	1.00	0.5	–	0	0	0.47	0.05
Lunulospora curvula	1.00	–	–	–	0	–	0	0	0.25	0.01
Magdalaenaea sp.	–	0	0	0	0	0	0	0	0#	0.01
Margaritispora aquatica	0.33	0	–	0	0	–	0.14	0	0.08	0.04
Porocladium aquaticum	0	–	–	–	0	–	1.00	0	0.25	0.01
Sporidesmium fuscum	0	0	0.5	0	0.14	–	0.14	0.75	0.22	0.12
Taeniolella typhoides	0	–	–	–	–	–	0	0	0#	0.01
Tetrachaetum elegans	1.00	–	–	–	0	–	0	0	0.25	0.01
Tetracladium breve	1.00	–	–	1.00	–	–	1.00	0	0.75	0.01
T. marchalianum	0.88	0.9	0.57	0.75	0.8	0.86	0.64	0.42	0.73	0.67
T. maxilliforme	0	0	–	0	–	–	0	0	0#	0.01
T. setigerum	0.45	0.17	0.17	0.57	0.4	0.5	0.19	0.17	0.33	0.19
Tricellula aquatica	0	0	–	0	0	0	0.2	0	0.03	0.03
Tricladium angulatum	0.84	1.00	0.44	0.71	0.73	0	0.22	0.19	0.52	0.34
T. biappendiculatum	–	0	0	0	0	0	0	0	0#	0.01
T. gracile	0.5	–	0	–	0.4	–	0.33	0	0.25	0.01
T. splendens	0.6	0	0	0	0.25	0	0	0.29	0.14	0.03
Tricladium sp.	0	–	–	–	0	–	1.00	0	0.25	0.02
? *Trinacrium* sp.	1.00	0	1.00	–	0.75	0	0.4	0.2	0.48	0.03
Triscelophorus monosporus	0.86	–	1.00	–	0.43	1	0.2	0.57	0.68	0.08
Triscelophorus sp.	0	0	–	0	0	–	0	0.5	0.08	0.01
Tumularia aquatica	–	0	–	–	–	0	0	0	0#	0.01
T. tuberculata	0	0	–	–	–	–	0	–	0#	0.01
Vargamyces aquaticus	0.84	0	0.5	0.25	0.38	0	0.1	0.36	0.3	0.16
Varicosporium delicatum	–	0	–	–	–	–	1.00	0	0.33	0.01
V. elodeae	0.33	0.25	0	0	0	0	0.5	0	0.14	0.02
V. tricladiiforme	0	1.00	–	–	0.25	–	0.89	0	0.43	0.08
Ypsilina graminea	0.25	0	0	0	0	0	0	0	0.03	0.03
Mean CC	0.5	0.21	0.43	0.31	0.26	0.29	0.3	0.24		
Total number of fungal species	30	12	18	15	22	9	29	25		
Number of pooled samples containing the substrate	87	15	20	17	62	10	63	76		

AL, *Alnus glutinosa*; B, *Betula pendula*; P, *Populus* spp.; Q, *Quercus robur*; S, *Salix* spp.; T, *Tilia cordata*; G, grass blades; W, woody substrates.

#, Fungus encountered on unidentified, minor or unusual substrates only.

–, Fungal species and substrate type have not been detected together in any watercourse.

0, Fungal species and substrate type have been detected in the same watercourse(s) but no colonization was observed.

assemblages on different types of plant litter in Belarus watercourses and to determine whether any substrate specificity or preferences occur.

MATERIALS AND METHODS

Ninety-two watercourses located in the Minsk region, the Berezinsky Biosphere Reserve, the National Park 'Belovezhskaya Pushcha', and protected area 'Golubyje Ozera' were examined between 1992–99. Watercourses were mainly streams flowing through plains or hilly areas of the Belarus Moraine Ridge and hence belonged to the catchment basins of the Baltic or Black Sea. Samples were taken only once from most streams, but 2–12 times from selected (9) streams. Attempts were made to collect 5 submerged decaying substrates of each litter type present at a particular site. Foam was also collected to detect species that might not be encountered on substrates, but that exist in the watercourse. Pooled samples consisted of all substrates and foam collected from a single locality at a particular time. Samples were taken back to the laboratory where substrates were rinsed with tap water and incubated singly in standing distilled water in Petri dishes for a few days at room temperature (20–22 °C) and in a refrigerator (*ca* 4 °) to induce sporulation; foam subsamples were examined under compound microscope. Detached conidia were identified and in some cases isolated in pure culture to confirm identification (Webster & Descals 1981, Descals 1997).

To solve problems when dealing with both fungal and substrate frequencies, a colonization coefficient (CC) was computed for each fungal species and substrate type. CC is defined as the number of pooled samples in which a given substrate is colonized by a particular species, divided by the number of pooled samples in which the given substrate and fungal species were both observed (but the fungus was not necessarily colonizing that substrate, i.e. aquatic hyphomycete may be detected on another substrate or in foam of the sample). Minor substrates that were encountered in less than 10 of 146 of the pooled samples were excluded. Frequency of occurrence on substrates in pooled samples (FOS; cases of occurrence in foam were excluded) was calculated for each aquatic hyphomycete to indicate whether the species was rare (FOS < 0.02). FOS is defined as the number of pooled samples in which a particular fungal species was observed, divided by the total number of pooled samples (146). Principal component analysis and cluster analysis were carried out to analyse classification of common substrates with respect to CC. Statistical packages STATISTICA 4.3 and SYSTAT 5.04 were used.

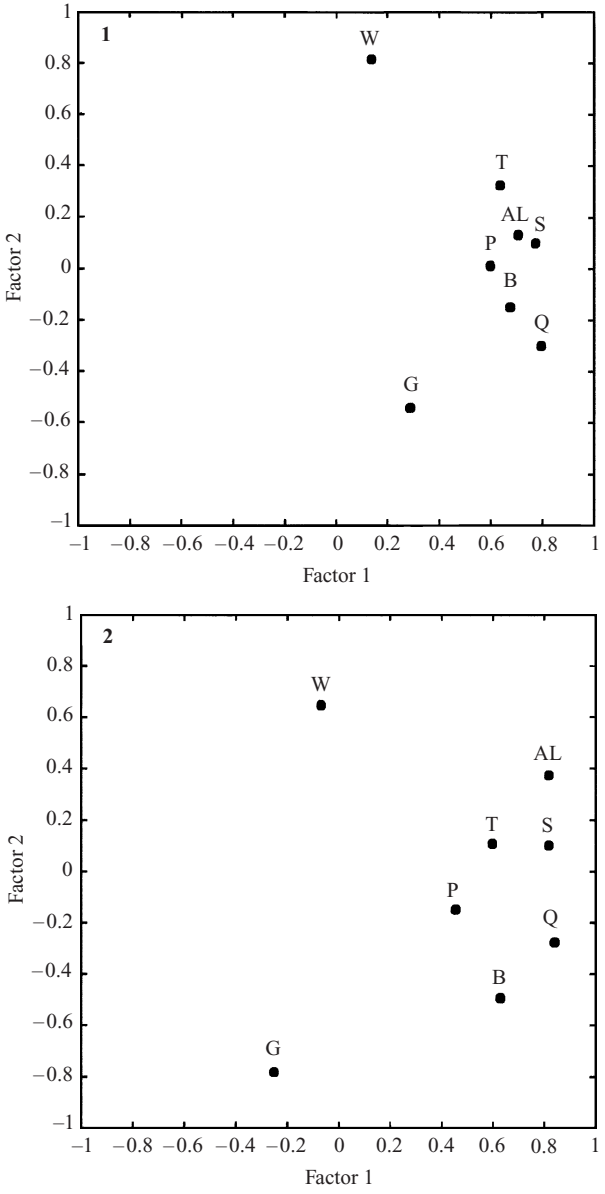
RESULTS

Altogether, 52 species of aquatic hyphomycetes were detected using the substrate incubation technique (Table 1; unknown species were omitted). Some species were new records for Belarus, 4 species appeared new (Gulis & Marvanová 1998, 1999), 2 have not been validly published yet (*Anguillospora* sp. and *Tricladium* sp.; Gulis 1999). The highest FOS (Table 1) values were for *A. longissima* (0.76), *T. marchalianum* (0.67), and *A. acuminata* (0.59). On the other hand, 42% of the species appear to be relatively rare (FOS < 0.02). To some extent that may be due to the lack of long-term observations in Belarus watercourses. Aquatic hyphomycetes were commonly encountered on leaf litter of *Alnus glutinosa*, *Salix* spp.

Table 2. Aquatic hyphomycetes on minor and unusual substrates.

	Tree leaf litter				Other substrates									
	Ac	Ul	Fr	Rh	Fi	Nu	Eq	Pol	Pot	Al	Uf	Pin	Pic	Dl
Total number of fungal species	13	10	9	5	5	5	4	4	3	3	3	3	1	1

Ac, *Acer* spp.; Ul, *Ulmus* spp.; Fr, *Fraxinus excelsior*; Rh, *Rhamnus cathartica*; Fi, *Filipendula* sp.; Nu, *Nuphar lutea*; Eq, *Equisetum* spp.; Pol, *Polygonum* sp.; Pot, *Potamogeton* spp.; Al, *Alium cepa* (scales); Uf, unidentified fern; Pin, *Pinus silvestris* (needles); Pic, *Picea abies* (cone); Dl, dead larvae of invertebrates.



Figs 1–2. Substrates ordination with respect to the first two factors of principal component analysis. **Fig. 1.** Raw data set. **Fig. 2.** Reduced data set. For abbreviations of substrates see Table 1.

and *Populus* spp.; 30, 22 and 18 species, respectively. Unexpectedly high species diversity was found on grass blades and wood (29 and 25 species, respectively). Some rare species were found only on these substrates: *P. aquaticum*, *Tricladium* sp., and *V. delicatum* on grass blades; *Anguillospora* sp., *Dimorphospora foliicola*, and *Triscelophorus* sp. on wood; and *Filosporella* spp. on both substrates). Some aquatic hyphomycetes (including undescribed taxa) were found on minor or unusual substrates (Table 2) especially in slow flowing waters.

The mean CC was higher for alder than for any other leaf species and lowest for birch and wood (Table 1). Species with the highest mean CC (if rare species with FOS < 0.02 are excluded) were 'true' aquatic hyphomycetes (*A. longissima*, *T. marchalianum*, and *T. monosporus*). These taxa are well adapted for aquatic environments. Species often encountered in terrestrial habitats (*Camposporium pellucidum*, *Varicosporium elodeae*, *Ypsilina graminea*) and *Heliscella stellata* have the lowest mean CC on submerged plant litter.

The results of principal component analysis of the raw data set (8 substrate types and 52 aquatic hyphomycetes) are presented in Fig. 1. The first three factors created by the analysis accounted for 38, 15.1 and 12.7% of the total variance, respectively. In an attempt to reach a better separation of plant litter, aquatic hyphomycetes with FOS < 0.02 (i.e. rare), those with the highest mean CC (> 0.6, i.e. fungi with low substrate selectivity) and 'terrestrial' species (*C. pellucidum*, *Fusarium cavispermum*, *Trinacrium* sp.) were removed (reduced data set, 23 fungal species). However, this did not change the ordination significantly (Fig. 2), the first three factors accounted for 38.4, 19.3 and 14.2% of the total variance. Calculations made with qualitative data (absence/presence of fungi on substrates) gave poorer ordination but with the same trends (wood and grass blades were clearly separated in all cases; data not shown).

The results of cluster analysis (raw data set) again suggested separation of tree leaf litter from grass blades and wood (Fig. 3). Analysis made with the reduced data set gave comparable results.

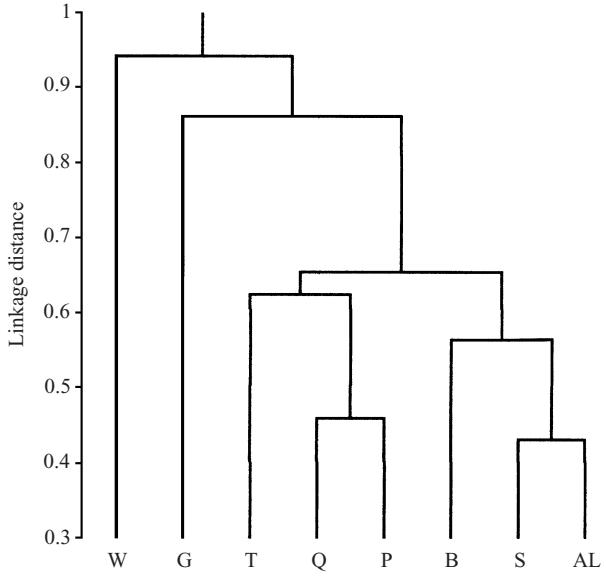


Fig. 3. Dendrogram showing the results of the UPGMA clustering of the common substrates. Distance: 1-Pearson *r* computed on the colonization coefficients (raw data set). For abbreviations of substrates see Table 1.

DISCUSSION

The main difficulty in assessing occurrence of fungal species on different substrates is to choose an appropriate method of calculation. If one chooses raw frequencies of occurrence then presence of a given fungal species on a particular substrate 'could be just as well a matter of change as of substrate preference' (Shearer & Webster 1991). Substrates themselves have different frequencies of occurrence in watercourses and, consequently, in samples that were used for assessing fungal occurrence patterns. For this reason the colonization coefficient described above was used in the present study.

Some examples of substrate preference in certain aquatic hyphomycete species have been already reported, however, no cases of absolute specificity have been documented. In a study on an Australian stream, Thomas, Chilvers & Norris (1992) demonstrated that of the ten most frequent aquatic hyphomycete species, seven showed significant preference for either disks of *Acacia* phyllodes or *Eucalyptus* leaves. They concluded that for most substrates it was possible to recognize them by the associated fungi. They also noted remarkable differences in fungal assemblages of leaves, bark and wood of the same plant species. In Spanish streams, *Lunulospora curvula* demonstrated clear preference for eucalypt *vs* alder leaves and this was attributed to differences in leaf chemical composition (Chauvet *et al*. 1997). Strong preference of *Tetracladium marchalianum* for alder leaves was noted in Hungarian (Gönczöl 1989) and Swedish streams (Bengtsson 1983). In the latter case this was also confirmed by laboratory experiments and assumed to be due to a combination of chemical composition of leaves and enzymatic equipment of the fungus. However, in Belarus watercourses, *T. marchalianum* exhibited a very high CC on most types of tree leaf litter (Table 1). Some signs of substrate preferences have been found among *Tetrachaetum elegans* genotypes from different plant genera assessed with RAPD analysis (Charcosset & Gardes 1999). It is also known that there are some differences in fungal colonization patterns between corticate and decorticate twigs (Shearer & Webster 1991, Gönczöl & Révay 1993) but no differences were found between tree species. Fabre (1996) concluded that in Pyrenean streams species richness and diversity of the aquatic hyphomycete community correlated with those of the riparian tree communities. However, he attributed this to a parallel structuring of both communities by environmental factors, in particular elevation.

In the present study, results of the principal component analysis (Figs 1–2) and cluster analysis (Fig. 3) demonstrate that it is possible to ordinate plant litter types by means of their fungal assemblages, suggesting substrate preferences in some species. One of the possible explanations of plant litter distribution along the F1 axis (Figs 1–2) is the size of substrate units. Twigs and grass blades have a low surface area on which aquatic hyphomycete conidia could be trapped. In addition, Lindsey & Glover (1976) demonstrated that flat

surfaces (as leaf lamina) are more efficient in trapping conidia than rod-like traps (i.e. twigs). Bärlocher & Schweizer (1983) found a significant correlation between the cumulative number of aquatic hyphomycetes and initial area of leaf squares they colonized. Sanders & Anderson (1979) demonstrated a similar correlation between the total number of fungal species and size of submerged wood blocks. Each particular grass blade or twig usually bears fewer aquatic hyphomycete species than occurs on any leaf. But a pair of twigs or grass blades recovered from a stream may support quite different fungal assemblages in contrast to leaf litter on which they are more uniform. Colonization of such small resource units is to some extent a matter of chance; in addition, there are some signs of succession on wood (Shearer 1992). This may result in higher cumulative number of fungal species than that from tree leaf litter (Table 1).

The distribution of leaf species along the F2 axis (Figs 1–2) seems to be closely related to their breakdown rates. Webster & Benfield (1986) summarized data concerning breakdown rates of various leaf species that were grouped by family. The following sequence according to the breakdown rates may be constructed with respect to the leaf species treated in the present study (in parentheses): *Tiliaceae* (*Tilia*) > *Betulaceae* (*Alnus*, *Betula*) > *Salicaceae* (*Salix*, *Populus*) > *Poaceae* + *Cyperaceae* (leaf blades) > *Fagaceae* (*Quercus*). It is also known that breakdown rate depends on the chemical composition of leaves, in particular lignin and tannins content (negative correlation; Suberkropp, Godshalk & Klug 1976, Webster & Benfield 1986, Gessner & Chauvet 1994), and perhaps positively correlates with initial nitrogen content (Webster & Benfield 1986; but see Gessner & Chauvet 1994). For example, alder leaves have a high N and low lignin content and, consequently, high breakdown rate; the opposite is true for oak. Note that CC values for these types of leaf litter are quite different for some common aquatic hyphomycete species (*Alatospora acuminata*, *Anguillospora longissima*, *Clavariopsis aquatica*, *Clavatospora longibrachiata*, etc.; Table 1); in addition, some species that occurred on alder leaf litter were absent from oak (e.g. *Heliscella stellata*, *Margaritispora aquatica*, *Triscelophorus monosporus*). This resulted in good separation of these substrates (Figs 1–2) suggesting substrate preferences in some aquatic hyphomycetes. The chemical composition of alder leaves favours colonization by aquatic hyphomycetes and may also explain the highest mean CC and number of fungal species on this substrate (Table 1).

It is more difficult to interpret the position of woody substrates on Figs 1–2. In the present study only small pieces of twigs (no longer than 10 cm and 2–8 mm diam) were collected. Thus, the area of such substrate unit was low, but surface/volume ratio was relatively high in comparison with other types of woody debris. Wood decomposes much more slowly than leaves mainly due to the high lignin content and low surface/volume ratio (Shearer 1992). It seems that the breakdown rate for such specimens should be higher than generally assumed for wood, but not so high so as to explain such ranking of wood with respect to the F2 axis (Figs 1-2).

Long-lasting substrates such as woody debris favour colonization by species which are capable of defending captured resources, in particular, by the production of antimicrobial compounds (Wicklow 1981). If species which are rare in this study are excluded, then *Fusarium cavispermum*, *Sporidesmium fuscum*, and *Anguillospora longissima* demonstrate the highest CC on wood. These species have been reported as having antimicrobial effects (Harrigan *et al*. 1995, Gulis & Stephanovich 1999).

Révay & Gönczöl (1990) pointed out significant differences between fungal communities associated with twigs and leaves and reported unusually high percentage of scolecosporous species from wood. Species with filiform conidia (*Anguillospora* spp., *Filosporella* spp., *F. cavispermum*, and *S. fuscum*) were also very frequent on wood and grass blades in Belarus watercourses (Table 1). These species may also dominate aquatic hyphomycete communities of temperate forest streams in summer when leaf litter is mostly unavailable. It is known that there are some differences in fungal communities between forested streams and those passing through areas of sparse riparian vegetation (Shearer & Webster 1985, Metwalli & Shearer 1989). The latter should harbour aquatic hyphomycetes adapted to grass blades, macrophytes, and perhaps also woody debris which was moved from upstream forested sites and retained here.

The results of this study demonstrate that some substrates support relatively specific aquatic hyphomycete assemblages and it is possible to ordinate plant litter types by means of their fungal complexes. This suggests selective colonization by fungi, i.e. substrate preferences at least in some species. Aquatic hyphomycete assemblages on wood, grass blades and tree leaf litter differ considerably, whereas fewer differences were found among types of leaf litter. Further studies should pay more attention to substrates other than tree leaf litter which presumably support specific fungal assemblages.

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