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Species diversity of freshwater hyphomycetes in some streams of Pakistan. III. Autumnal colonization of freshwater hyphomycetes on bait leaves

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Significantly more species of freshwater hyphomycetes colonized bait leaves of alder (16 species) and willow (14 species) during early submersion period (1 wk) than those of oak (8 species). Production of conidia was also higher on alder and willow leaves than on oak leaves. Higher amounts of dry mass were lost from the alder (28.6%) and willow leaves (29.4%) than from the oak leaves (18.7%). Rapid loss of dry mass was accompanied by rapid development of a fungal community. Fungal species took a longer time (6 wk) to reach their peak of occurrence on oak than on willow and alder leaves (3–4 wk). *Flagellospora curvula* dominated the assemblages of freshwater hyphomycetes on alder and willow leaves, and *Lunulospora curvula* dominated the assemblage on oak leaves. The freshwater hyphomycete community showed higher values of species diversity (H value) on oak leaves than on alder and willow leaves.

Key Words——species diversity; freshwater hyphomycetes; autumnal colonization; leaf baits.

Since the discovery of freshwater hyphomycetes by Ingold (1942) as the characteristic fungal flora associated with decaying leaf litter in streams, a considerable body of literature has accumulated on the distribution and ecology of these fungi (Bärlocher, 1992b; Suberkropp, 1992). These fungi occur in a variety of habitats and different geographical locations (Bärlocher and Rosset, 1981; Webster and Descals, 1981). They are well adapted in their conidial morphology (Ingold, 1979; Webster, 1981) to colonize and exhibit physiological adaptations (Suberkropp and Klug, 1981) for plant litter degradation in running waters.

Several methods have been used to estimate the abundance of freshwater hyphomycetes. These are: 1) Estimation of conidia suspended in the water. This can be done by a) the filtration technique (Iqbal and Webster, 1973), and b) direct examination of conidia with an inverted microscope (Müller-Haeckel and Marvanová, 1979). 2) Examination of persistent foam or scum which develops below rapids and traps conidia (Ingold, 1942). Trapping of conidia in artificial foam may remove some of the difficulties in interpreting the community structure based on conidia trapped in natural foam (Iqbal, 1993). 3) Detection of fungi on substrata by a) examination of naturally colonized decaying submerged leaves (Conway, 1970; Gönczol, 1975; Iqbal et al., 1979; Suberkropp and Klug, 1974; Eggenschwiler and Bärlocher, 1983); and b) examination of communities developing on standardized leaf packs exposed to streams at different times of the year (Suberkropp, 1984; Shearer and Webster, 1985a,b,c). Because the rates of decay and developmental speed of these fungi vary with the season (Suberkropp, 1984; Iqbal, 1994), however, different developmental stages may be recorded even if identical exposure times are chosen (Gessner et al., 1993).

Similar patterns of fungal dominance have been detected on a leaf species at a site during consecutive seasons (Suberkropp, 1984; Gessner et al., 1993). Different leaf species, e.g., oak and hickory (Suberkropp, 1984), banyan, coffee, mango, rubber and cashew (Sridhar and Kaveriappa, 1989), show marked differences in colonization and breakdown rates. Bärlocher (1992a) compared the degradation and colonization in three leaf species under similar conditions. Species colonizing bait leaves do not reach their peak of occurrence at the same time and predried leaves are degraded and colonized by freshwater hyphomycetes under submerged conditions more quickly than fresh leaves (Bärlocher, 1991, 1992a; Gessner, 1991). In the present study, which is based on the leaf pack baiting technique, standardized leaf packs (Shearer and Webster, 1985a) were retrieved at different repeated intervals.

The present study was undertaken (1) to characterize colonization patterns by freshwater hyphomycetes, (2) to determine the time taken by a freshwater hyphomycete community to mature, and (3) to document the differences in communities developing on the baits of different leaf species.

The differences in the fungal assemblages detected on bait leaves of alder, willow and oak have been expressed in terms of species diversity—a statistical abstraction with two components reflecting the numbers of species (richness) and the distribution of individuals of all species equitability (evenness) in a community at a particular site (MacArthur, 1965; McIntoch, 1967). The structure of the freshwater hyphomycetes community

can be summarized by the index of species diversity measured by the Shannon-Wiener function (H) (Llyod and Ghelardi, 1964).

Materials and Methods

Description of the sampling site The sampling site, Jabori (grid reference SX270681) on the Jabori Canal, is situated in the Dadar area, Siran Valley (Iqbal, 1992, 1994). The Jabori Canal originates from the River Siran approximately 0.5 km upstream of the sampling site. As the river makes a semi-circular turn around the village of Jabori, it strikes a hill and some of the river water is diverted into a contour, which with time has been converted into a canal. This canal flows parallel to the river. It is about 1 m wide and 40-45 cm deep. A thin layer of a mixture of clay and sand is deposited on the gravelly and stony bed of the canal. The banks are covered with herbaceous vegetation (for other details, e.g., riparian vegetation, see Iqbal, 1992; and for physico-chemical characters of the canal such as temperature, pH, EC, nitrates and phosphates present in the canal water, see Iqbal, 1994).

Collection method Leaf pack baiting: All leaves of each species used in this study were collected from single trees of *Alnus glutinosa* (L.) Gaertn, *Salix babylonica* L., and *Quercus dilatata* Lindl. Branches were gently shaken and shed leaves were collected. As *A. glutinosa* is not a component of the riparian vegetation on the canal, alder leaves were collected from a tree in Jhelum Valley (Kashmir). Leaves with no fungal invasion were dried at 20°C for 7 d. These packs of air-dried leaves of alder, willow and oak were placed separately in nylon nets with a mesh size of 1.5 mm. The leaves in packs were sewn and arranged in a single layer so as not to cover each other.

The leaf packs of each leaf species supported on a metal frame were attached to house-bricks and placed in the canal with packs facing against the flow of the canal. One leaf pack of each species was retrieved at intervals of one wk (see legend of Fig. 2). Leaves were rinsed in the canal water to remove adhering debris after retrieval and transported back to the laboratory in a thermos flask. In the laboratory, the leaves were rinsed in sterilized distilled water and each leaf was cut into nine 1 cm^2 discs. Three discs from each leaf were aerated singly at 20°C in McCartney bottles, each containing 15 ml of distilled water. After 24 h, the resulting spore suspension was passed through an 8 μm pore size filter. Conidia on filters were fixed, stained and processed after Iqbal and Webster (1973). Production of conidia has been used as an estimate of species presence. To confirm the identities of conidia difficult to identify on the filter, three discs/leaf that had been aerated and incubated for 24 h were examined simultaneously with the filtering of spore suspension for comparison and for counts of conidia/disc.

Frequencies and relative frequencies of occurrence for each species were calculated according to procedures of Shearer and Webster (1985a) and Iqbal (1994).

The leaf material (3 discs/leaf) not used for the analysis of freshwater hyphomycete community was dried at 105°C and weighed to the nearest 0.001 g.

To compare the freshwater hyphomycete communi-

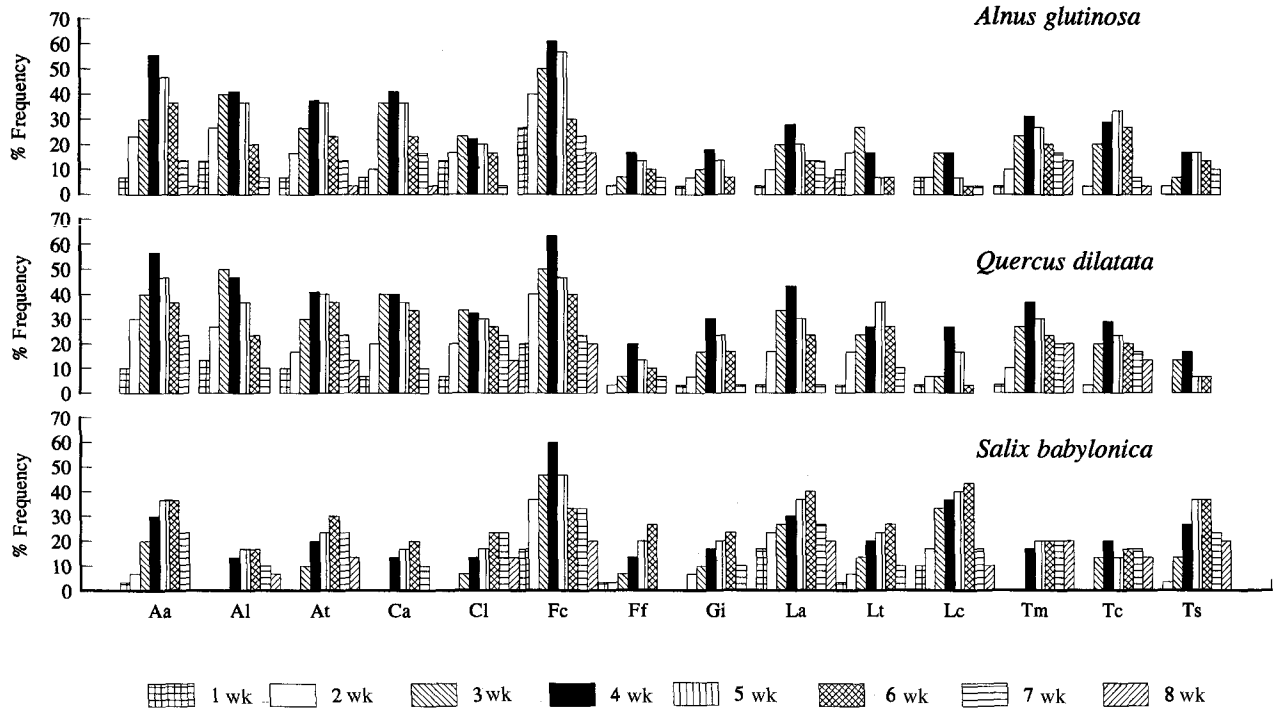

Fig. 1. Autumnal colonization patterns of dominant freshwater hyphomycetes on baited leaves of three species submerged in the Jabori Canal. For acronyms of species see Table 1.

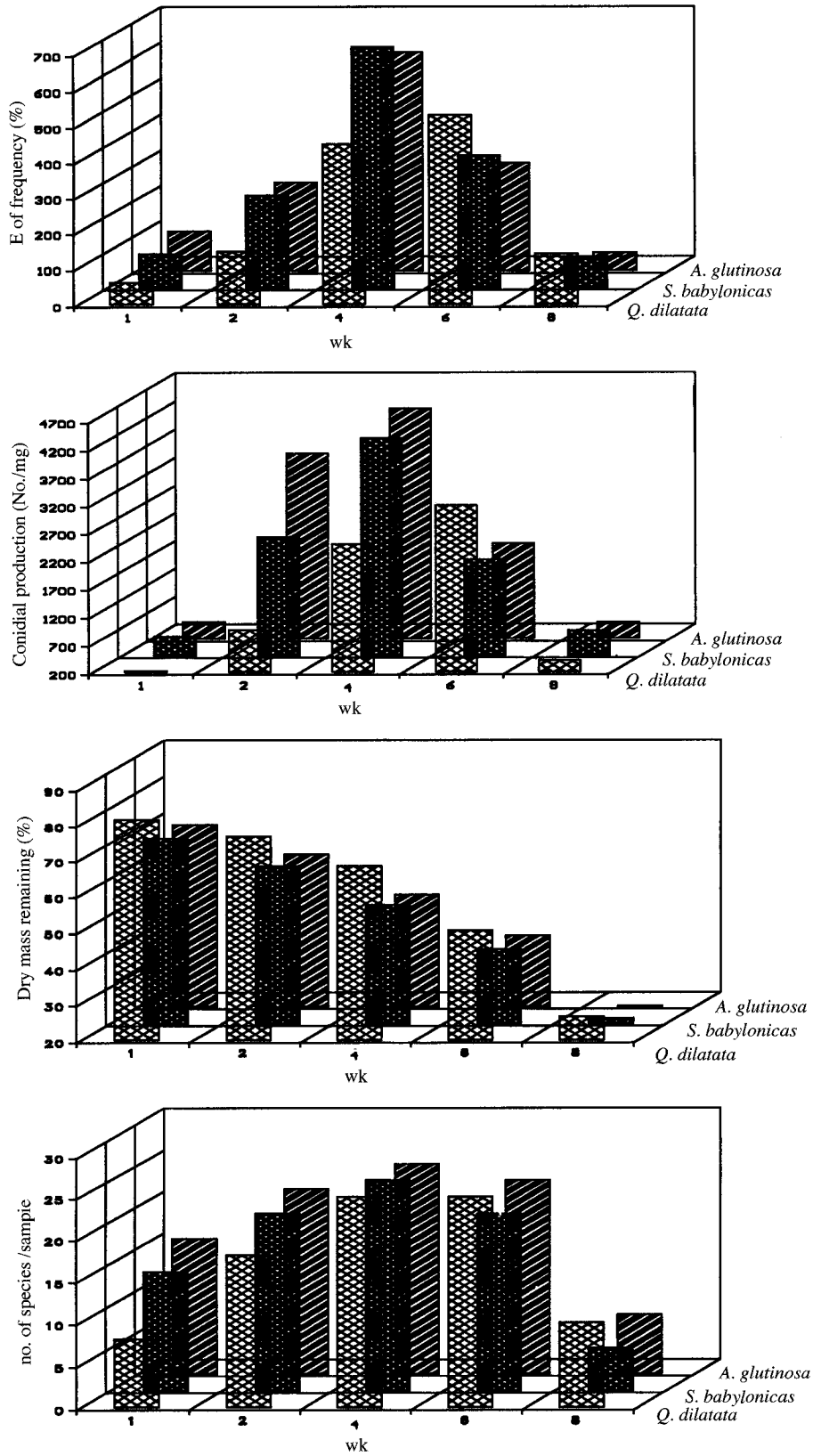

Fig. 2. Mass loss of leaf litter of *Alnus glutinosa*, *Salix babylonica* and *Quercus dilatata*, conidial production, number of species colonizing and the sum of their frequencies at different exposure times in autumn (October-November) in the Jabori Canal.

ties detected on these three leaf species immersed in the Jabori Canal in autumn, Sorensen's two indices were calculated (Mueller-Dombois and Ellenberg, 1974): one Sorensen's index is defined as the number of common species found in two communities divided by the average number of species of the two communities, and the second index is calculated from the sum of the lower percentages of occurrence in either of the two communities.

An index of diversity in freshwater hyphomycete communities was calculated by the Shannon-Weiner function

$$H = -\sum_{i=1}^{s} (Pi) \log_2 Pi$$

where H=index of species diversity, s=number of species and P*i*=proportion of total sample belonging to *i* th species (Krebs, 1978).

To document the distribution of frequency of occurrence of species among communities on three bait leaf species in the Jabori Canal, evenness (E) was calculated by $E = H/H_{max}$ where H_{max}=species diversity under conditions of maximal evenness. Evenness can also be defined as the ratio between the observed species diversity (H) and maximum species diversity (H_{max}), as $E = H/H_{max} = H/\log_2 S$ (Krebs, 1978), where S=number of species in the community.

Results

The details of range of pH, temperature, EC, nitrates and phosphates in the canal water have been given in Iqbal (1994).

The colonization pattern of species of freshwater hyphomycetes on leaves of *A. glutinosa*, *S. babylonica* and *Q. dilatata* submerged in the Jabori Canal (Figs. 1, 2)

Table 1. Relative frequency and frequency of occurrence (%), H-diversity and E (evenness) values of freshwater hyphomycetes on baited leaves of *Salix babylonica*, *Alnus glutinosa* and *Quercus dilatata* in the Jabori Canal in autumn (12 October–11 November).

Acronyms	Species	*Salix babylonica*			*Alnus glutinosa*			*Quercus dilatata*		
		F	RF	(P*i*) ($\log_2 pi$)	F	RF	(P*i*) ($\log_2 pi$)	F	RF	(P*i*) ($\log_2 pi$)
Aa:	*Alatospora acuminata*	56.7	0.067	0.3003	56.7	0.094	0.3003	36.7	0.067	0.2611
	A. constricta	16.7	0.025	0.1328	16.7	0.027	0.1405	6.7	0.012	0.0764
	Anguillospora crassa	16.7	0.025	0.1328	16.7	0.027	0.1405	3.3	0.006	0.0441
Al:	*A. longissima*	46.7	0.069	0.2660	41.1	0.067	0.2611	16.7	0.030	0.1514
	Articulospora proliferata	16.7	0.025	0.1328	16.7	0.027	0.1405	16.7	0.030	0.1514
At:	*A. tetracladia*	41.1	0.061	0.2458	37.7	0.062	0.2404	30.00	0.055	0.2298
	Bacillispora aquatica	13.3	0.020	0.1126	16.7	0.027	0.1405	16.7	0.030	0.1514
	B. inflata	10.0	0.015	0.0906	13.3	0.022	0.1209	13.3	0.024	0.1288
Ca:	*Clavariopsis aquatica*	40.0	0.059	0.2408	41.1	0.067	0.2189	20.0	0.036	0.1724
Cl:	*Clavatospora longibrachiata*	32.2	0.048	0.2102	22.2	0.036	0.2013	23.3	0.043	0.1949
	Dactylella aquatica	10.0	0.015	0.0906	16.7	0.027	0.1209	13.3	0.024	0.1288
	Dimorphospora foliicola	16.7	0.025	0.1328	16.7	0.027	0.1405	16.7	0.030	0.1514
Fc:	*Flagellospora curvula*	63.3	0.094	0.3205	61.1	0.100	0.3321	33.3	0.061	0.2458
Ff:	*F. fusarioides*	20.0	0.030	0.1328	16.7	0.027	0.1405	26.7	0.049	0.2129
Gi:	*Geniculospora inflata*	30.0	0.045	0.2013	17.8	0.029	0.1724	23.3	0.043	0.1949
	Heliscus lugdunensis	13.3	0.020	0.1126	16.7	0.027	0.1209	16.7	0.030	0.1514
La:	*Lemonniera aquatica*	43.3	0.064	0.2537	27.8	0.045	0.2611	40.0	0.073	0.2757
	L. centrosphaera	23.3	0.035	0.1690	13.3	0.027	0.1405	20.0	0.036	0.1724
	L. filiformis	16.7	0.025	0.1328	16.7	0.027	0.1405	13.3	0.024	0.1288
Lt:	*L. terrestris*	26.7	0.040	0.1856	16.7	0.027	0.1405	26.7	0.049	0.2129
Lc:	*Lunulospora curvula*	26.7	0.040	0.1856	16.7	0.027	0.1405	43.3	0.079	0.2890
	Margaritispora aquatica	10.0	0.015	0.0906	13.3	0.022	0.1209	16.7	0.030	0.1514
Tm:	*Tetracladium marchalianum*	36.7	0.054	0.2272	31.1	0.051	0.2072	20.0	0.036	0.1724
Tc:	*Tricladium chaetocladium*	28.9	0.043	0.1949	28.9	0.047	0.1478	16.7	0.030	0.1514
Ts:	*Triscelophorus monosporus*	16.7	0.025	0.1328	16.7	0.027	0.1405	36.7	0.067	0.2611
Σ=				4.4267			4.3726			4.4636
Total no. of species			25			25			25	
Σ frequency of occurrence			672.4			611.2			546.8	
E (equitability evenness) $E = H/\log_2 S$			0.953			0.942			0.961	

was influenced by type of bait leaves and the duration of immersion.

Production of conidia was recorded on the leaves of alder and willow after 4 d of submersion in autumn. *Flagellospora curvula* and *Anguillospora longissima* colonized and produced conidia on willow and alder leaves. *Dimorphospora foliicola* and *Clavatospora longibrachiata* colonized and fruited on willow and alder leaves, respectively, after 4 d of submersion of these leaves in the Jabori Canal, although conidial production was light (10–20 conidia/species). An exposure of 1 wk of these two leaf species resulted in dense (50-∞ conidia/species) sporulation by *F. curvula* and *A. longissima*. Other species, *Alatospora acuminata, Articulospora tetracladia, Bacillispora aquatica, Clavariopsis aquatica, C. longibrachiata, D. foliicola, Geniculospora inflata, Heliscus lugdunensis* (alder only), *Lemonniera aquatica, Lemonniera centrosphaera* (alder only), *Lemonniera terrestris, Lunulospora curvula, Margaritispora aquatica* and *Tetracladium marchalianum* also sporulated, though sparsely (5–20 conidia/species) (Fig. 2). *Flagellospora curvula* dominated this assemblage.

The colonization of alder and willow leaves after 2 wk was characterized by dense sporulation of *F. curvula* and *A. longissima*, and an increase in frequency of occurrence of several other species (*A. acuminata, C. aquatica, C. longibrachiata, A. tetracladia, L. aquatica, L. terrestris, T. marchalianum*). *Tricladium chaetocladium* and other species occurred sparsely (Fig. 1). Several of these species (5 on willow and 7 on alder) remained important components of the communities in the canal even in later stages of decay (8 wk) (see Table 3). Communities on leaves of alder and willow were saturated, i.e., no new colonizer species were added after 3 wk of immersion in the canal. However, after 4 wk in the canal, communities had matured and most of the species colonizing in the first week had assumed significant importance.

In this study, a freshwater hyphomycete community comprising 25 species developed on the leaves of *Q. dilatata* after 6 wk (Table 1). Eight species colonized the oak leaves in the first week. *Flagellospora curvula, L. aquatica* and *L. curvula* produced conidia frequently (more than 20 conidia/species). Sporulation by other species was sparse. Other species joined the early colonizers after 2 wk. However, *F. curvula* dominated this assemblage. Twenty-one species colonized the leaves after a submersion period of 3 wk (Fig. 2). *Flagellospora curvula, L. curvula, L. aquatica, A. acuminata* produced conidia abundantly. The freshwater hyphomycete community was saturated with species on oak leaves submerged for 4 wk. *Flagellospora curvula* reached its peak of occurrence in 4 wk (Fig. 1). *Anguillospora longissima, Anguillospora crassa* and *T. marchalianum* appeared on the leaves after 4 wk (Fig. 1). The freshwater hyphomycete community matured on the leaves of *Q. dilatata* after 6 wk. As this community matured, more than 50% of the dry mass of leaves was lost (Fig. 2). *Lunulospora curvula* reached its peak of occurrence after 6 wk and it dominated this community (Fig. 1).

Flagellospora curvula took 4 wk to reach its peak of occurrence on the three leaf species. Several other species, e.g., *A. acuminata, A. longissima, A. tetracladia, C. aquatica, C. longibrachiata, G. inflata, H. lugdunensis, L. aquatica, L. curvula, T. chaetocladium* and *Triscelophorus monosporus* took a longer period (6 wk) to reach peak of occurrence on oak leaves (Fig. 1). *Anguillospora longissima, C. aquatica* and *C. longibrachiata* took 3 wk to reach their peak of occurrence on willow leaves (Fig. 1).

Weight loss of bait leaves occurred more slowly in oak leaves than in those of alder and willow (Fig. 2). Weight loss was positively correlated with the rate of colonization of freshwater hyphomycete species. Eight species colonized the oak leaves submerged for 1 wk, as against 14 on willow and 16 on alder leaves (Fig. 2). The sum of frequencies of all species—another measure of colonization showed a positive correlation with the leaf decay of these three leaf species. Similarly, numbers of conidia of species colonizing leaves were positively correlated with the rate of weight loss of leaves (Fig. 2).

The 10 top-ranking species on each of the three leaf species formed a group of 14 freshwater hyphomycetes.

Table 2. Relative frequencies (RF) and percentage frequency (F%) of occurrence of the ten top-ranking freshwater hyphomycetes on leaf baits of *Alnus glutinosa, Salix babylonica* and *Quercus dilatata*.

A. glutinosa			*S. babylonica*			*Q. dilatata*		
Species	F (%)	RF	Species	F (%)	RF	Species	F (%)	RF
1. *F. curvula*	61.1	0.10	1. *F. curvula*	63.3	0.094	1. *L. curvula*	43.3	0.079
2. *A. acuminata*	55.5	0.091	2. *A. acuminata*	56.7	0.084	2. *L. aquatica*	40.0	0.073
3. *A. longissima*	41.1	0.067	3. *A. longissima*	46.7	0.069	3. *A. acuminata*	36.7	0.067
4. *C. aquatica*	41.1	0.067	4. *L. aquatica*	43.3	0.064	4. *T. monosporus*	36.7	0.067
5. *A. tetracladia*	37.7	0.062	5. *A. tetracladia*	41.1	0.061	5. *F. curvula*	33.3	0.061
6. *T. marchalianum*	31.1	0.051	6. *C. aquatica*	40.0	0.059	6. *A. tetracladia*	30.0	0.055
7. *T. chaetocladium*	28.9	0.047	7. *T. marchalianum*	36.7	0.054	7. *L. terrestris*	26.7	0.049
8. *L. aquatica*	27.8	0.045	8. *C. longibrachiata*	32.2	0.048	8. *F. fusarioides*	26.7	0.049
9. *C. longibrachiata*	22.2	0.036	9. *G. inflata*	30.0	0.045	9. *C. longibrachiata*	23.3	0.043
10. *G. inflata*	17.8	0.029	10. *T. chaetocladium*	28.9	0.043	10. *G. inflata*	23.3	0.043

Table 3. Occurrence of species of freshwater hyphomycetes on the three leaf species submerged in the canal for 8 wk.

Species	Leaf species		
	Willow	Oak	Alder
Heliscus lugdunensis	−	−	+
Alatospora constricta	−	+	−
Anguillospora longissima	−	+	+
Articulospora tetracladia	+	+	−
Clavatospora longibrachiata	+	+	−
Dactylella aquatica	−	−	+
Flagellospora curvula	+	+	+
Lemonniera aquatica	−	+	−
Lunulospora curvula	−	+	+
Tetracladium marchalianum	+	+	+
Tricladium chaetocladium	+	+	+
Triscelophorus monosporus	−	+	−
Total number of species	5	10	7

The 10 top-ranking species on the leaves of alder and willow were the same, but these differed in ranking (Table 2). *Flagellospora curvula*, *A. acuminata* and *A. longissima* were the first 3 top-ranking species in communities on the alder and willow leaves (Table 2). The freshwater hyphomycete community on oak leaves was dominated by *L. curvula*. *Triscelophorus monosporus*, *Flagellospora fusarioides* and *L. terrestris* among the 10 top-ranking species. These species occurred less frequently on alder and willow leaves (Table 2). *Anguillospora longissima*, *T. marchalianum* and *T. chaetocladium*, which were among the 10 top-ranking species on alder and willow, occurred less frequently on oak leaves (Table 1).

Bait leaves of the three tree species were completely skeletonized after 8 wk. Skeletonized leaves of willow, alder and oak bore 5, 7 and 10 species, respectively. *Flagellospora curvula*, *T. marchalianum* and *T. chaetocladium* were present on the skeletonized leaves of all the three species (Fig. 2). *Alatospora constricta*, *A. longissima* (Fig. 1), *Dactylella aquatica*, *L. curvula* (Fig. 2, Table 3) were present on the skeletonized leaves of alder and oak. *Articulospora tetracladia* and *C. longibrachiata* occurred on the skeletonized leaves of willow and oak (Fig. 1). *Heliscus lugdunensis*, *L. aquatica* and *T. monosporus* were present on the skeletonized leaves of oak only (Table 3).

The three assemblages of freshwater hyphomycetes colonizing leaves of *S. babylonica*, *A. glutinosa* and *Q. dilatata* were similar and showed 100% Sorensen's similarity index on the basis of the presence and absence of species. This similarity index fell to 91.4% on the basis of relative frequency of species between communities on alder and willow leaves, to 81.2% between communities on willow and oak leaves and to 80.2% between communities on alder and oak leaves (Table 4).

Species diversity among the freshwater hyphomycete communities on the leaves were calculated using the Shannon-Weiner function (H). The freshwater

Table 4. Similarity indices between communities on bait leaves of alder, willow and oak submerged in the Jabori Canal. Values given within brackets indicate the similarity indices based on the relative frequencies of the species forming communities.

	Alder	Willow	Oak
Alder	—	100 (91.4)	100 (80.2)
Willow		—	100 (81.2)

hyphomycete community on oak leaves showed higher species diversity (4.4636) than on willow (4.4267) and on alder leaves (4.3726) (Table 1). The community showing higher species diversity (H values) also showed higher values of evenness (E). The freshwater hyphomycete community on oak leaves showed higher E values (0.9610) than on willow (0.953) and on alder leaves (0.942) (Table 1).

Discussion

In the development of freshwater hyphomycete communities on leaves, fungi which colonize early typically persist throughout leaf degradation (Bärlocher, 1982b; Chamier and Dixon, 1982; Bärlocher and Schweizer, 1983; Shearer and Webster, 1985a; Shearer and Webster, 1991). Rankings of the dominant species may change through time (Suberkropp and Klug, 1976) but successional replacement of species is generally not observed. If species colonize leaves late in the degradation process, they are generally rare in occurrence (Bärlocher, 1982a). Thus, the fungi which 'colonize' a leaf soon after it enters a stream appear to have a major impact on the development of the community in that leaf. Suberkropp (1984) demonstrated in exchange experiments that prior establishment by fungi such as *L. curvula*, *Flagellospora penicillioides* modified the ability of other fungi, e.g., *F. curvula*, *L. aquatica* and *A. acuminata* to colonize bait leaves at temperatures that would have otherwise resulted in their dominance.

The species composition of fungal communities on different types of deciduous leaves is generally similar when leaves are colonized in the same stream during the same time period (Bärlocher and Kendrick, 1974; Chamier and Dixon, 1982; Chergui and Pattee, 1988; Shearer and Lane, 1983; Sridhar and Kaveriappa, 1989; Suberkropp and Klug, 1976). However, dominance patterns in the fungal communities on the leaves usually differ (Gönczol, 1975, 1989; Rossi et al., 1983). Similarly, communities developing on different types of leaves frequently exhibit quantitative differences (i.e., in frequencies, or densities of species), particularly on leaves with contrasting rates of breakdown: e.g., *T. marchalianum* is less abundant on oak leaves than on other more readily degraded deciduous leaves such as alder and willow (Figs. 1, 2) (Suberkropp and Klug, 1976). This appears to be caused by reduced capacity of *T. marchalianum* to degrade oak leaves (Bärlocher and Kendrick, 1974; Butler

and Suberkropp, 1986). On the other hand, the colonization and occurrence of *F. curvula* were the same on all substrata (Fig. 1). These differences among the communities of different leaf species are correlated with their breakdown rates (Fig. 1). The weight loss from the submerged leaves is also caused by the leaching out of water-soluble extracts which inhibit the radial growth of these fungi. Extracts from different leaf species differ in their inhibitory effect (Bärlocher, 1992a). A faster decay of the bait leaves of alder and willow resulted in colonization by a higher number of fungi as pioneer species, and development of the community took place within 4 wk of immersion. A delay in the weight loss of leaves caused by low temperature in winter (Iqbal, unpublished; Gessner et al., 1993) or the slow rate of breakdown in oak leaves results in slowing down the development of a mature community. Rate of weight loss also influenced the conidial production. More conidia were produced on leaves of alder and willow than on oak leaves at various residence periods in the canal. These changes in rates of weight loss of leaves of different species affects not only the colonization but also the time taken by a community to mature on different leaf species. The development of a freshwater hyphomycete community can be divided into 3 stages. 1) An assemblage of a few species in the beginning as the pioneer species/early colonizers. 2) A mature community with most of the species reaching their peak of frequencies resulting in the maximum value of Σ of frequencies (Fig. 2). This stage coincides with 50% or more mass loss of the leaf. 3) A reduction in dry mass of leaf accompanied by a low number of species and impoverished production of conidia. This is in line with the findings of Chamier and Dixon (1982) that, for a given habitat, the rate of leaf decay is defined by a characteristic fungal assemblage and vice-versa.

The results shown in Figs. 1 and 2 generally confirm the observations of Suberkropp and Klug (1976) and Bärlocher (1982b) that the activity of freshwater hyphomycetes declines during later stages in the decay of a substrate. The number of species occurring on the skeletonized leaves of the three tree species fell to 5 (on willow), 7 (on alder) and 10 (on oak). Three species, i.e., *F. curvula, T. marchalianum* and *T. chaetocladium* were present on the skeletonized leaves of the three species (submerged for 8 wk). Ingold (1944) noted, besides the seasonal occurrence of *L. curvula*, the growth of some species were associated with skeletonized submerged leaves.

It has been argued (Warcup, 1965) that techniques for characterization of fungal populations should be based on an estimate of actively growing mycelium. This is certainly true if one wants to know which species is responsible for the disappearance of certain substrates (e.g., wood-destroying fungi) or which species will provide the bulk of biomass supporting consumers of high trophic levels. The reproductive phase is equally relevant and probably more traceable by present methods. In fact, the ultimate success of any organism can be measured by the number of viable descendants it leaves during its lifetime (Bärlocher, 1992a).

Communities on *A. glutinosa* and *S. babylonica* leaves showed 100% similarity on the basis of presence and absence of species and 91.4% similarity on the basis of relative frequency. Alder leaves have frequently been used in colonization studies because they are readily colonized by a wide variety of freshwater hyphomycete species (Shearer and Webster, 1985b). Willow leaves were found to be as good as alder leaves as indicated by the similarity indices.

Communities on oak and other leaves are similar in their species richness and differ in species diversity measured by the Shannon-Weiner function (H). Higher values of Shannon-Weiner function H indicates higher species diversity and higher E values for the community on oak leaves is indicative of a more even or equitable distribution among species. This component also shows greater species diversity. Retention of phenolics in slowly degrading leaves of oak (Gessner, 1991; Bärlocher, 1991, 1992a) caused colonization of oak leaves by fewer (8) species than on alder (16) and willow (14). However, the delayed weight loss was accompanied by a higher number of species after longer residence periods of oak leaves (Fig. 2) than on alder and willow leaves, which lose weight quickly. The number of species declined with longer immersion periods (4-6 wk), resulting in an impoverished community of fewer species, e.g., 5 in willow and 7 in alder, with low frequency of occurrence (Figs. 1, 2).

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