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# Species diversity of freshwater hyphomycetes in some streams of Pakistan. II. Seasonal differences of fungal communities on leaves

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Significantly more fungal species colonized leaves in summer, spring and autumn during the first week of submersion than in winter. Higher amounts of dry leaf mass were lost in summer, spring and autumn than in winter. Rapid loss of dry mass was accompanied by rapid development of a fungal community. Colonization and sporulation rates varied with each fungal species. Maximum frequency of occurrence of fungal species were reached earlier (3–4 weeks) in summer and spring communities than in communities of autumn (4 weeks) and winter (6 weeks). More conidia were produced per milligram plant material in winter and autumn than in summer and spring. *Flagellospora curvula* dominated the communities in autumn, winter and spring while *Lunulospora curvula* dominated the summer community. The occurrence of rich fungal communities on leaves in four seasons is due to the availability of deciduous substrata contributed by the riparian vegetation, supplemented with seasonal addition of wheat and rice straw and enrichment of the canal water with phosphates and nitrates washed down from the bordering fields.

Key words: freshwater hyphomycetes, seasonal differences, species diversity

## INTRODUCTION

Freshwater hyphomycetes are well adapted to colonize (Ingold 1979, Webster 1981) and degrade plant litter in running waters (Suberkropp & Klug 1981). Considerable literature has accumulated on the ecology of freshwater hyphomycetes associated with decaying leaf litter in streams and rivers (Bärlocher 1992).

The structure of freshwater hyphomycete communities colonizing and sporulating on submerged leaves in a stream can be determined quickly by examination of randomly sampled leaves. However, naturally colonized leaves differ in age and substrate quality at the time of sampling due to the pulsed input of deciduous leaves to temperate streams, coupled with marked differences in breakdown rates among leaf species. Seasonal differences in communities of freshwater hyphomycetes, based on the examination of naturally colonized leaves, may be caused by differences in fungal development as a result of changes in substrate quality or by differences in general environmental conditions such as temperature and inoculum potential (Iqbal 1994).

The communities detected on naturally colonized submerged leaves and on bait leaves generally do not differ in species composition. However, differences in the number of individuals of each species (abundance) change their ranking in these communities (Shearer & Webster 1985c, Iqbal 1994).

Leaf pack baits provide standardized, homogeneous substrata which can be manipulated with respect to time and location (Shearer & Webster 1985a). However, due to differences in rate of decay and developmental speed of fungi with season (Suberkropp 1984), different developmental stages can still be recorded even if identical exposure times are chosen (Gessner *et al*. 1993). To avoid this, standardized leaf packs should not only be exposed at different times of the year, but also retrieved at frequent intervals.

Differences in the freshwater hyphomycete communities detected in different seasons have been expressed in terms of species diversity — a statistical abstraction with two components reflecting the number of species (richness) and the distribution of individuals of all species (equitability or evenness) in a community at a particular site (Llyod & Ghelardi 1964). The structure of the freshwater hyphomycete community can be summarized by Index of species diversity measured by the Shannon-Wiener function ($H$).

A greater number of species or a more even or equitable distribution among species will both increase species diversity measured by the Shannon-Wiener function. Communities with a similar richness may differ in diversity, depending upon the distribution of individuals among the species. Diversity indices reflect changes in overall information content, rather than enumerate upon changes of an individual species composition. Where one species is completely replaced by another, the diversity value would remain constant, yet the change of species may be indicative of significant environmental modification.

The Jabori Canal, rich in $NO_3$ and $PO_4$, with smooth water flow, low temperature (6–16°C) and sheltered by a rich riparian vegetation contributing deciduous substrata in autumn, supplemented by seasonal agricultural products such as wheat and rice straw from the neighbouring fields (Iqbal 1994), provided an ideal habitat to study the community of freshwater hyphomycetes, its colonization patterns, the correlation of colonization by these fungi with the degradation of leaf mass, and to document differences in communities developing on *Salix* leaf baits in four different seasons.

## MATERIALS AND METHODS

### Sampling site

The sampling site, the Jabori bridge (grid reference SX 270681) on the Jabori Canal is situated on the River Siran 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. The canal flows parallel to the river making a semi-circular turn round the Village Jabori, following a contour. The canal is about 1 m wide and 40–45 cm deep. The gravelly and stony bed of the canal is covered by a thin mixture of clay and sand. Water flows smoothly, at 0.65 m/s. The banks are covered with herbaceous vegetation intermixed with grasses and trees. The frequency of occurrence of these trees and shrubs was estimated in 10-m-wide and 500-m-long strips on both sides from the sampling site moving upstreams and expressed on a scale of one asterisk (* = 1 to 5 plants in the two strips), and two asterisks (** = 6 to 10 plants in the two strips). The riparian vegetation consists of *Eriobotrya japonica* (Thunb.) Lindley*, *Pyrus malus* L.*, *Alnus nitida* Endl.*, *Pinus roxburghii* Sargent*, *Quercus incana* Roxb.*, *Q. dilatata* Lindle ex Royle*, *Prunus persica* (L.) Stokes*, *Populus nigra* L.**, *Salix babylonica* L.**, *S. tetrasperma* Roxb.**, *Aesculus indica* (Wall. ex Camb.) Hook.f.*, *Ficus palmata* Forssk.**, *Melia azedarach* L.**, *Zanthoxylum alatum* Roxb.*, *Lagerstroemia indica* L.*, *Rubus fruticosus* Hook.f. non L.** and *Berberis lycium* Royle**.

This canal has a richer deciduous riparian vegetation than the other streams of the area (see Iqbal 1992, 1994). The peak season of deciduous leaf litter fall is between mid September and early December. Some agricultural products such as wheat and rice straw, and leaves of other crops find their way into the canal. Branches of trees and shrubs of the riparian vegetation also fall into the canal.

The Jabori Canal is similar to other streams of the area except that some nitrates and phosphates are washed down/leached into the canal on its way through agricultural fields. The values of electrical conductivity range from 95–140 µS; $NO_3$ from 15–25 mg/l and $PO_4$ from 0.6 to 8.5 mg/l. The pH (5.9–6.9) of the canal is circumneutral. Temperature ranges from 6°C to 16°C (Iqbal 1994) (Fig. 1).

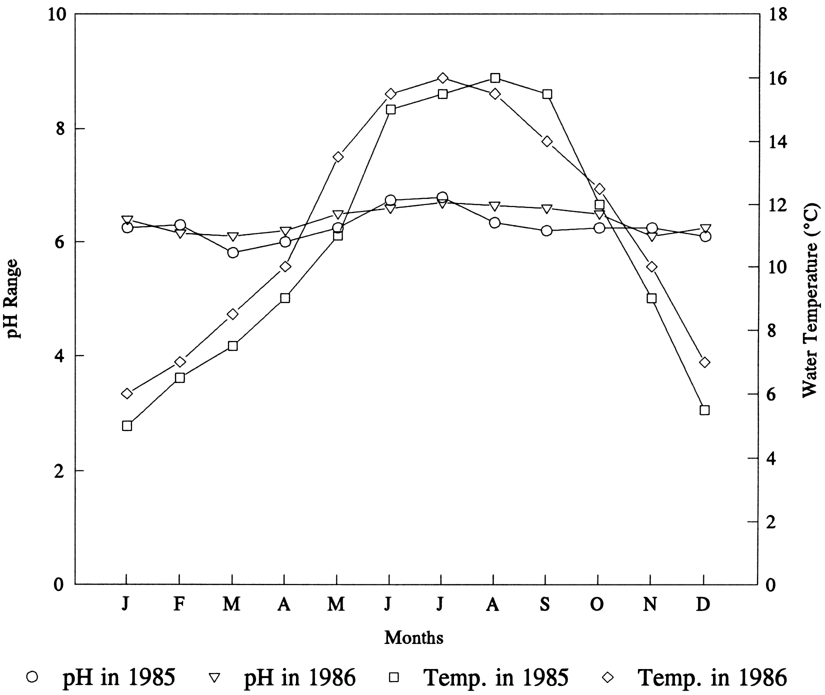


Fig. 1. pH and water temperature (°C) of the Jabori Canal in the years 1985 and 1986.

## Leaf pack baiting

Branches were gently shaken and yellowish brown leaves with no visible fungal invasion were selected from the shed leaves. Leaves thus collected in October were used as leaf packs for autumn (October–November) and winter (November–December), and those collected in November–December were used in spring (May–June) and summer (July–August) 1987. *Salix babylonica* is a component of riparian vegetation. All leaves used in this study were collected from one of the trees (sheltering the canal) from the Siran Valley. Leaves were dried at 20°C for 7 days. These air-dried leaves were packed in nylon nets with a mesh size of 1.5 mm. Ten such leaves of approximately equal length were sewn into packs and arranged in a single layer so as not to cover each other.

Eight to ten leaf packs supported individually on metal frames were attached to bricks which were placed in the canal in each season with packs facing against the flow of the canal water. These leaves (one leaf pack at a time) were removed from the canal at weekly intervals (see Fig. 2) throughout the four seasons (1986–1987).

These leaves were transported back to the laboratory separately in plastic bags in a thermos flask. In the laboratory the leaves were carefully rinsed and each leaf was cut up into 9 discs of 1 $cm^2$. Three discs from each leaf were aerated singly at 20°C in McCartney bottles each containing 15 ml distilled water. After 24 h, the resulting spore suspension was passed through an 8-µm pore size filter. To confirm the identities of conidia difficult to identify on the filter, 3 discs/leaf 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 fungal species were calculated according to procedures in Shearer and Webster (1985a) and Iqbal (1994). The leaf material (3 discs/leaf) not used for the analysis of freshwater hyphomycete communities was dried at 105°C and weighed to the nearest 0.001 g.

## Membrane filtration

The canal water was filtered to ascertain the relative contribution of each freshwater hyphomycete species to the conidial pool. Conidia from 5 l of the canal water were identified and counted according to the procedures of Iqbal and Webster (1973b).

## Trapping of conidia in artificial foam

An artificial foam trap was developed below rapids by adding detergent to the canal water. The amount of canal water passing through the foam trap in 5 min was about 500 l. The foam formed in the trap was collected in a beaker, allowed to settle and later fixed in FAA, dried and stained with 0.1% cotton blue in lactic acid (Iqbal 1993). The filters were processed as described by Iqbal and Webster (1973b). The conidia were identified and counted. Results were reported as relative frequencies (RF).

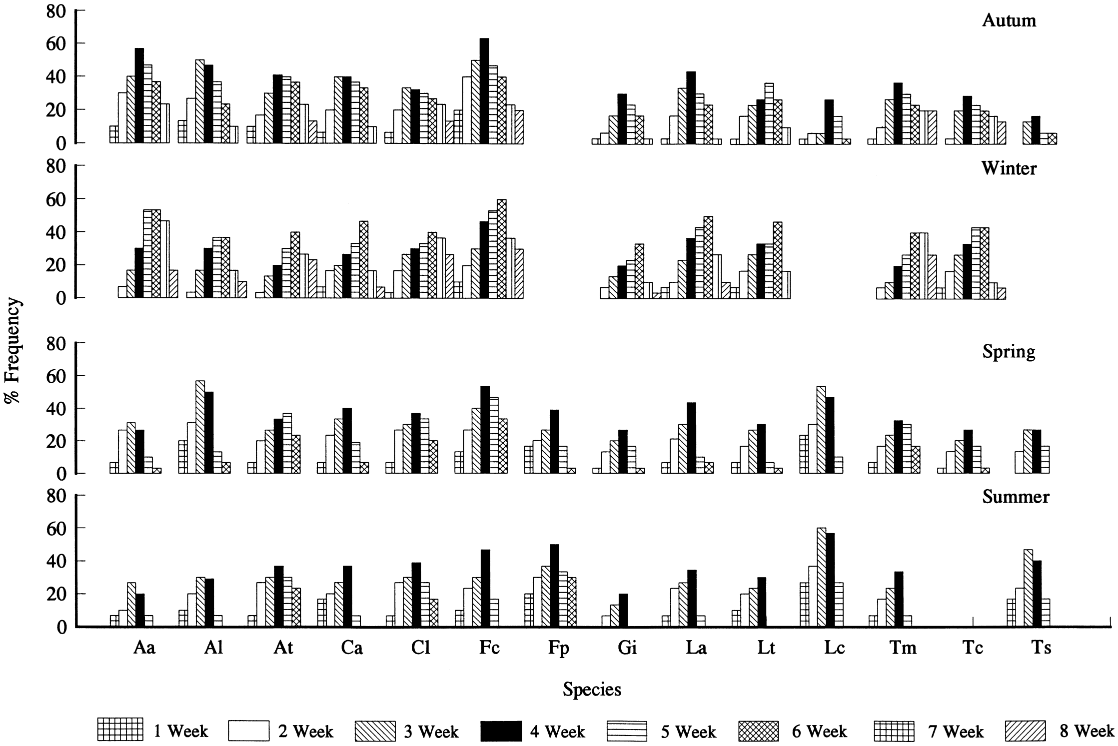


Fig. 2. Mass loss of *Salix babylonica* leaves, number of conidia/mg, number of species colonizing and the sum of occurrence frequency (%) of all species in the sample at different exposure times times over the four seasons in the Jabori Canal.

To compare the freshwater hyphomycete communities detected on the leaf baits immersed in the Jabori Canal in the four seasons of the year, Sørensen's two indices were calculated (Mueller-Dombois & Ellenberg 1974); Sørensen's index defined as the number of common species found in two communities divided by the average number of species in them. The second index was 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-Wiener function:

$$H = -\sum_{i=1}^{s} (p_1) \log_2 Pi \qquad (1)$$

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

To document the frequency distribution of species occurrence among communities on leaf baits in the four seasons in the Jabori Canal, equitability or evenness ($E$) was calculated by:

$$E = \text{Shannon-Wiener Index } H/H_{\max} \qquad (2)$$

where $H_{\max}$ = species diversity under conditions of maximal evenness = $\log_2 S$ (max. value when individuals evenly distributed among the species). $S$ = number of species in the community.

Equitability or evenness ($E$) can also defined as the ratio between the observed species diversity ($H$) and maximum species diversity ($H_{\max}$), as

$$E = H/H_{\max} \qquad (3)$$

where $E$ = equitability (range 0–1), $H$ = observed species diversity, $H_{\max}$ = maximum species diversity = $\log_2 S$, $E = H/H_{\max} = H/\log_2 S$.

# RESULTS

## Conidial pool in the Jabori Canal

Thirty-seven species were identified by the filtration method and the same number of species were trapped in the foam concentrate in October. Eight species of the ten top-ranking species detected by filtration and in the foam concentrate were identical. Species with tetraradiate conidia e.g., *Lemonniera aquatica* and *Geniculospora inflata* were trapped more frequently in the foam concentrate than those with conventional or sigmoid conidia i.e., *Dactylella aquatica* and *Flagellospora penicillioides* (see Iqbal 1993, 1994) (Table 1).

More species were identified by the filtration method and trapped in foam concentrate in autumn (37) and winter (38) than in spring (27) and summer (26). Seven to eight of the ten top-ranking species detected by these methods were identical (Tables 1–4). However, these species differed in their ranking (Tables 1–4). Conidia with conventional shape (*Dactylella aquatica*, *Margaritispora aquatica*), and cylindrical (*Heliscus lugdunensis*) and sigmoid (*Flagellospora penicillioides*) shapes occurred more frequently in the stream water than in the foam concentrate (Table 1). Conidia with tetraradiate shape such as *Clavatospora longibrachiata*, *Geniculospora inflata, Lemonniera aquatica*, *L. terrestris, Tetracladium chaetocladium* and *T. marchalianum,* which occurred less frequently in the canal water than in the foam, replaced species with conventional or cylindrical/sigmoid conidia by their higher trapping efficiency in the foam concentrate (see Iqbal 1993) (Tables 1–4).

### Mass losses of *Salix* bait leaves submerged in the Jabori Canal

More dry leaf mass was lost in summer (38.5%), spring (34.2%), and autumn (29.4%) than in winter (22.4%) on submersion of *Salix* leaf baits for 1 week in the Jabori Canal. Rapid mass loss was accompanied by a faster rate of colonization by freshwater hyphomycetes. Significantly more species in summer (20), spring (19) and autumn (14) than in winter (6) colonized *Salix* leaf baits submerged for 1 week in the Jabori Canal (Fig. 3). Numbers of conidia produced by species coloniz-

Table 1. Colonization of leaf baits of *Salix babylonica* by freshwater hyphomycetes showing relative frequency (RF), mean number of conidia $L^{-1}$ (mean) and relative frequency of conidia in stream water and in artificial foam, for the ten top-ranking species in the Jabori Canal at the time of leaf bait submersion (October) and retrieval (November). *N* = Number of species.

| October filtration $N$ = 37, Conidia $L^{-1}$ = 2680 | | | Bait leaves $N$ = 25 | | November filtration $N$ = 38, Conidia $L^{-1}$ = 3640 | | |
|---|---|---|---|---|---|---|---|
| Species | Mean | RF | Species | RF | Species | Mean | RF |
| *F. curvula* | 570 | 0.213 | *F. curvula* | 0.0941 | *F. curvula* | 0.267 | 0.267 |
| *A. longissima* | 502 | 0.187 | *A. acuminata* | 0.0843 | *A. longissima* | 0.102 | 0.102 |
| *L. curvula* | 469 | 0.175 | *A. longissima* | 0.0694 | *H. lugdunensis* | 0.051 | 0.051 |
| *H. lugdunensis* | 455 | 0.170 | *L. aquatica* | 0.0643 | *C. aquatica* | 0.040 | 0.040 |
| *A. acuminata* | 80 | 0.030 | *A. tetracladia* | 0.0641 | *A. acuminata* | 0.031 | 0.031 |
| *F. penicillioides* | 73 | 0.027 | *C. aquatica* | 0.0594 | *M. clavata* | 0.031 | 0.031 |
| *A. tetracladia* | 51 | 0.019 | *T. marchalianum* | 0.0545 | *T. marchalianum* | 0.030 | 0.030 |
| *C. aquatica* | 51 | 0.019 | *C. longibrachiata* | 0.0478 | *T. chaetocladium* | 0.029 | 0.029 |
| *D. aquatica* | 46 | 0.017 | *G. inflata* | 0.0446 | *A. tetracladia* | 0.025 | 0.025 |
| *C. longibrachiata* | 43 | 0.016 | *T. chaetocladium* | 0.0429 | *C. longibrachiata* | 0.025 | 0.025 |

| Artificial Foam | | Artificial Foam | |
|---|---|---|---|
| Species | RF | Species | RF |
| *A. tetracladia* | 0.084 | *A. acuminata* | 0.094 |
| *A. acuminata* | 0.081 | *C. longibrachiata* | 0.071 |
| *A. longissima* | 0.072 | *T. marchalianum* | 0.070 |
| *C. longibrachiata* | 0.072 | *T. chaetocladium* | 0.067 |
| *T. marchalianum* | 0.060 | *C. aquatica* | 0.066 |
| *F. curvula* | 0.052 | *A. longissima* | 0.060 |
| *C. aquatica* | 0.046 | *L. aquatica* | 0.060 |
| *L. aquatica* | 0.046 | *A. tetracladia* | 0.057 |
| *G. inflata* | 0.045 | *F. curvula* | 0.055 |
| *T. chaetocladium* | 0.045 | *G. inflata* | 0.051 |

ing leaves were higher in summer, spring and autumn coinciding with greater loss of mass of *Salix* leaf baits. The sum (∑) of frequencies (%) of all species, which is another measure of colonization, was significantly higher in summer (193.5), spring (150.0), autumn (93.1) than in winter (40.1) and coincided with the greater mass loss of bait leaves in the early submersion period.

## Colonization patterns of freshwater hyphomycetes on submerged bait leaves of *Salix*

Production of conidia was recorded on the *Salix* leaf baits after 4 days of submersion in autumn (October–November). *Flagellospora curvula*, *Anguillospora longissima* and *Dimorphospora foliicola* were observed but production of conidia was low. Exposure for one week resulted in dense sporulation of *Flagellospora curvula* and *Anguillospora longissima*. Some other species, *Alatospora acuminata*, *Articulospora tetracladia*, *Clavariopsis aquatica*, *Clavatospora longibrachiata*, *Geniculospora inflata*, *Lemonniera aquatica*, *L. terrestris*, *Lunulospora curvula* and *Tetracladium marchalianum* also sporulated though less profusely (Fig. 2).

Early stages of colonization (2 weeks' exposure) were characterised by a dense sporulation of *Flagellospora curvula* and the regular occurrence of nine other species (*Alatospora acuminata*, *Anguillospora longissima*, *Clavariopsis aquatica*, *Clavatospora longibrachiata*, *Articulospora tetracladia*, *Lemonniera aquatica*, *L. terrestris*, *Tetracladium marchalianum*, *Tricladium chaetocladium*) was scarce (Fig. 2). These species remained important components of the communities in the canal even in later stages of leaf decay. However, after 4 weeks in the canal, an additional 15 species had assumed significant importance with the

Table 2. Colonization of leaf baits of *Salix babylonica* by freshwater hyphomycetes showing relative frequency (RF), mean number of conidia $L^{-1}$ (mean) and relative frequency of conidia in stream water and in artificial foam for the ten top-ranking species in the Jabori Canal at the time of leaf bait submersion (November) and retrieval (December). $N$ = Number of species.

| November filtration $N$ = 37, Conidia $L^{-1}$ = 3640 | | | Bait leaves $N$ = 27 | | December filtration $N$ = 38, Conidia $L^{-1}$ = 4280 | | |
|---|---|---|---|---|---|---|---|
| Species | Mean | RF | Species | RF | Species | Mean | RF |
| *F. curvula* | 972 | 0.267 | *F. curvula* | 0.0833 | *F. curvula* | 1190 | 0.278 |
| *A. longissima* | 372 | 0.102 | *A. acuminata* | 0.0740 | *A. longissima* | 540 | 0.126 |
| *H. lugdunensis* | 186 | 0.051 | *L. aquatica* | 0.0694 | *H. lugdunensis* | 244 | 0.057 |
| *C. aquatica* | 145 | 0.04 | *C. aquatica* | 0.0648 | *L. aquatica* | 163 | 0.038 |
| *A. acuminata* | 113 | 0.031 | *L. terrestris* | 0.0648 | *L. terrestris* | 150 | 0.035 |
| *M. clavata* | 113 | 0.031 | *T. chaetocladium* | 0.0601 | *D. aquatica* | 140 | 0.032 |
| *T. marchalianum* | 109 | 0.03 | *A. tetracladia* | 0.0555 | *C. longibrachiata* | 133 | 0.031 |
| *T. chaetocladium* | 106 | 0.029 | *C. longibrachiata* | 0.0555 | *F. fusarioides* | 120 | 0.028 |
| *A. tetracladia* | 91 | 0.025 | *T. marchalianum* | 0.0555 | *A. acuminata* | 116 | 0.027 |
| *C. longibrachiata* | 91 | 0.025 | *A. longissima* | 0.0509 | *C. aquatica* | 112 | 0.026 |

| Artificial Foam | | Artificial Foam | |
|---|---|---|---|
| Species | RF | Species | RF |
| *A. acuminata* | 0.094 | *A. acuminata* | 0.075 |
| *C. longibrachiata* | 0.071 | *A. longissima* | 0.070 |
| *T. marchalianum* | 0.070 | *A. tetracladia* | 0.070 |
| *T. chaetocladium* | 0.067 | *F. curvula* | 0.068 |
| *C. aquatica* | 0.066 | *C. longibrachiata* | 0.065 |
| *A. longissima* | 0.060 | *L. terrestris* | 0.065 |
| *L. aquatica* | 0.060 | *T. chaetocladium* | 0.065 |
| *A. tetracladia* | 0.057 | *L. aquatica* | 0.061 |
| *F. curvula* | 0.055 | *T. marchalianum* | 0.052 |
| *L. terrestris* | 0.051 | *C. aquatica* | 0.051 |

result that by this time, communities included at least fourteen abundant species with a frequency of each species higher than 20% (Fig. 2). *Flagellospora curvula* took 4 weeks to reach its peak frequency of occurrence. *Anguillospora longissima*, *Clavariopsis aquatica* and *Clavatospora longibrachiata* achieved this in 3 weeks (Fig. 2). In autumn, a freshwater hyphomycete community took 4 weeks in the canal to develop. A twenty-five species-strong community of freshwater hyphomycetes on the bait leaves of *Salix babylonica* in autumn was characterised by abundance of the ten top-ranking species, *Flagellospora curvula*, *Alatospora acuminata*, *Anguillospora longissima*, *Lemonniera aquatica*, *Articulospora tetracladia*, *Clavariopsis aquatica*, *Tetracladium marchalianum*, *Clavatospora longibrachiata*, *Geniculospora inflata* and *Tricladium chaetocladium* (Table 5).

After the component species of the autumn community had reached the peak frequency of occurrence, about 50% of the leaf material was broken down. After 7 weeks, leaves were substantially degraded and sporulation was markedly reduced (Fig. 3).

In contrast to the developmental patterns in autumn, *Flagellospora curvula* colonized and produced conidia abundantly after 1 week's immersion of leaf pack baits in winter (November) (Fig. 2). *Clavariopsis aquatica*, *Lemonniera aquatica*, *L. terrestris*, *Tricladium chaetocladium* and *Clavatospora longibrachia* also sporulated though scarcely. With an increase in the residence period of leaf baits, the number of the colonizing species increased. Twenty-three species colonized the leaf baits after 2 weeks (Fig. 3). This stage was characterized by profuse sporulation of *Flagellospora curvula* and the regular occurrence of nine other

Table 3. Colonization of leaf baits of *Salix babylonica* by freshwater hyphomycetes showing relative frequency (RF), mean number of conidia $L^{-1}$ (mean) and relative frequency of conidia in stream water and in artificial foam for the ten top-ranking species in the Jabori Canal at the time of leaf bait submersion (May) and retrieval (June). *N* = Number of species.

| May filtration *N* = 27, Conidia $L^{-1}$ = 980 | | | Bait leaves *N* = 26 | | June filtration *N* = 26, Conidia $L^{-1}$ = 310 | | |
|---|---|---|---|---|---|---|---|
| Species | Mean | RF | Species | RF | Species | Mean | RF |
| *L. curvula* | 160 | 0.163 | *F. curvula* | 0.0810 | *L. curvula* | 52 | 0.166 |
| *F. curvula* | 158 | 0.161 | *A. longissima* | 0.0760 | *F. penicillioides* | 43 | 0.137 |
| *F. penicillioides* | 102 | 0.104 | *L. curvula* | 0.0709 | *F. curvula* | 37 | 0.118 |
| *A. longissima* | 101 | 0.103 | *L. aquatica* | 0.0658 | *A. longissima* | 34 | 0.110 |
| *H. lugdunensis* | 99 | 0.101 | *C. aquatica* | 0.0608 | *H. lugdunensis* | 24 | 0.077 |
| *D. aquatica* | 60 | 0.061 | *F. penicillioides* | 0.0591 | *D. aquatica* | 20 | 0.065 |
| *L. aquatica* | 34 | 0.035 | *C. longibrachiata* | 0.0557 | *C. aquatica* | 12 | 0.038 |
| *L. terrestris* | 26 | 0.026 | *A. tetracladia* | 0.0506 | *T. marchalianum* | 11 | 0.033 |
| *C. aquatica* | 26 | 0.026 | *T. marchalianum* | 0.0489 | *L. terrestris* | 10 | 0.032 |
| *A. tetracladia* | 23 | 0.023 | *L. terrestris* | 0.0456 | *C. longibrachiata* | 9 | 0.028 |

| Artificial Foam | | Artificial Foam | |
|---|---|---|---|
| Species | RF | Species | RF |
| *A. longissima* | 0.093 | *T. marchalianum* | 0.085 |
| *L. aquatica* | 0.085 | *C. longibrachiata* | 0.082 |
| *L. terrestris* | 0.073 | *A. longissima* | 0.072 |
| *C. aquatica* | 0.068 | *L. aquatica* | 0.072 |
| *T. marchalianum* | 0.065 | *A. tetracladia* | 0.070 |
| *A. tetracladia* | 0.065 | *L. curvula* | 0.067 |
| *L. curvula* | 0.065 | *C. aquatica* | 0.066 |
| *C. longibrachiata* | 0.063 | *F. curvula* | 0.062 |
| *F. curvula* | 0.059 | *L. terrestris* | 0.058 |
| *F. penicillioides* | 0.048 | *F. penicillioides* | 0.050 |

species, namely *Clavariopsis aquatica*, *Clavatospora longibrachiata*, *Lemonniera terrestris*, *Tricladium chaetocladium*, *Lemonniera aquatica*, *Alatospora acuminata*, *Geniculospora inflata*, *Tetracladium marchalianum* and *Articulospora tetracladia*. These ten species remained dominant in the community in the later stages of decay. After an immersion period of 3 weeks, 27 species colonized and fruited on the leaves (Fig. 3). At this point, the community had 12 dominant species with a frequency of occurrence > 10%. No new colonizers appeared on the leaf baits in subsequent samples. However, there was an increase in the frequency of occurrence in most of the species (Fig. 2). The community developed after 6 weeks in winter. At this stage, the species forming the community had their peak frequency of occurrence. More than 50% of the leaf material had degraded by this time (Fig. 3). After 7 weeks of submersion, freshwater hyphomycete species showed a fall in the frequency of occurrence. This was accompanied by the further degradation of leaf baits. After 8 weeks, the leaf baits were substantially broken down and sporulation was markedly reduced. At this stage, 14 species appeared on these much-degraded leaves with low frequencies of occurrence (Fig. 3).

The colonization of leaf pack baits submerged in spring (May) and summer (July–August) was characterised by a higher number of species (19–20) (Fig. 3) and greater frequency of occurrence after 1 week of immersion than in other seasons (Fig. 3).

*Lunulospora curvula*, *Anguillospora longissima*, *Flagellospora penicillioides* and *F. curvula* colonized and sporulated abundantly after 1 week's submersion of leaf baits in spring. *Alatospora acuminata*, *Articulospora tetracladia*, *Clavariopsis aquatica*, *Clavatospora longibrachiata*, *Lemonniera aquatica*, *L. terrestris* and *Tetracla-*

Table 4. Colonization of leaf baits of *Salix babylonica* by freshwater hyphomycetes showing relative frequency (RF), mean number of conidia $L^{-1}$ (mean) and relative frequency of conidia in stream water and in artificial foam for the ten top-ranking species in the Jabori Canal at the time of leaf bait submersion (July) and retrieval (August). *N* = Number of species.

| July filtration *N* = 22, Conidia $L^{-1}$ = 680 | | | Bait leaves *N* = 23 | | August filtration *N* = 26, Conidia $L^{-1}$ = 860 | | |
|---|---|---|---|---|---|---|---|
| Species | Mean | RF | Species | RF | Species | Mean | RF |
| *F. penicillioides* | 111 | 0.162 | *L. curvula* | 0.0892 | *L. curvula* | 141 | 0.164 |
| *L. curvula* | 92 | 0.134 | *F. penicillioides* | 0.0786 | *F. penicillioides* | 124 | 0.144 |
| *F. curvula* | 85 | 0.125 | *F. curvula* | 0.0734 | *F. curvula* | 117 | 0.136 |
| *D. aquatica* | 83 | 0.121 | *T. monosporus* | 0.0629 | *A. longissima* | 87 | 0.101 |
| *A. longissima* | 69 | 0.101 | *C. longibrachiata* | 0.0612 | *H. lugdunensis* | 67 | 0.077 |
| *H. lugdunensis* | 66 | 0.096 | *C. aquatica* | 0.0577 | *T. monosporus* | 66 | 0.076 |
| *T. monosporus* | 36 | 0.052 | *L. aquatica* | 0.0541 | *T. marchalianum* | 37 | 0.042 |
| *C. aquatica* | 34 | 0.050 | *T. marchalianum* | 0.0523 | *C. aquatica* | 34 | 0.040 |
| *T. marchalianum* | 24 | 0.035 | *L. terrestris* | 0.0471 | *L. aquatica* | 23 | 0.026 |
| *L. aquatica* | 13 | 0.019 | *A. longissima* | 0.0454 | *D. aquatica* | 22 | 0.025 |

| Artificial Foam | | Artificial Foam | |
|---|---|---|---|
| Species | RF | Species | RF |
| *T. marchalianum* | 0.102 | *T. monosporus* | 0.092 |
| *T. monosporus* | 0.088 | *A. longissima* | 0.088 |
| *C. longibrachiata* | 0.075 | *T. marchalianum* | 0.084 |
| *C. aquatica* | 0.070 | *C. aquatica* | 0.076 |
| *L. aquatica* | 0.068 | *C. longibrachiata* | 0.075 |
| *L. curvula* | 0.068 | *L. terrestris* | 0.070 |
| *A. longissima* | 0.067 | *L. curvula* | 0.061 |
| *F. penicillioides* | 0.060 | *L. aquatica* | 0.052 |
| *F. curvula* | 0.059 | *F. penicillioides* | 0.051 |
| *L. terrestris* | 0.052 | *F. curvula* | 0.050 |

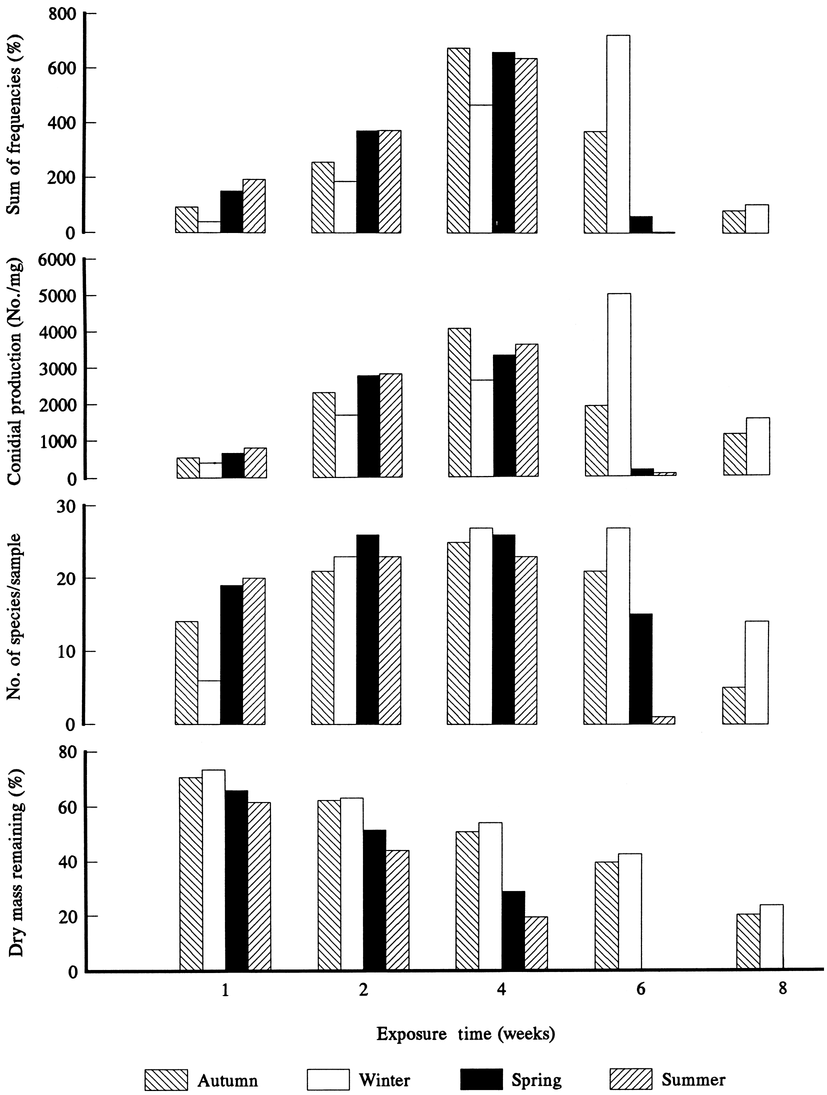


Fig. 3. Seasonal colonization patterns of dominant freshwater hyphomycetes on bait leaves of *Salix babylonica* submerged in the Jabori Canal. For acronyms of species, see Table 5.

*dium marchalianum* also colonized and sporulated. After an immersion of 2 weeks, the community had 26 species. This community included 14 abundant species each with a frequency of occurrence >10%. With an increase in the residence period of the leaf baits in the canal, the number of species remained constant. However, there was an increase in frequency of occurrence in most of the species (Fig. 2). The freshwater hyphomycete community developed after 4 weeks of submersion in the canal, however, *Anguillospora longissima*, *Lunulospora curvula* and *Triscelophorus monosporus* reached their peaks after 3 weeks of submersion in spring (Fig. 2). About 70% of the leaf material was broken down after 4 weeks' submersion of the leaves (Fig. 3). This was accompanied by lowering of the frequency of occurrence (%) of freshwater hyphomycete species (Fig. 2).

Twenty species colonized the leaves submerged for 1 week in the canal in summer (Fig. 3). *Lunulospora curvula*, *Flagellospora penicillioides*, *Triscelophorus monosporus*, *Clavariopsis aquatica* and *Clavatospora longibrachiata* were abundant species. *Anguillospora longissima* and *Flagellospora curvula* occurred frequently. Each of these species had a frequency of occurrence greater than 10%. Twenty-three species colonized the leaf baits after 2 weeks. *Lunulospora curvula*, *Flagellospora penicillioides*, *Clavatospora longibrachiata*, *Articulospora tetracladia*, *Anguillo-*

*spora longissima*, *Clavariopsis aquatica*, *Flagellospora curvula* and *Triscelophorus monosporus* showed dense sporulation. With an increase in residence time, the frequency of occurrence of each species increased. The community was saturated with species after two weeks' submersion of the bait leaves. The community developed after 4 weeks of submersion, however, *Anguillospora longissima*, *Alatospora acuminata*, *Lunulospora curvula* and *Triscelophorus monosporus* reached their peak of occurrence after 3 weeks' submersion of bait leaves. *Lunulospora curvula*, *Flagellospora penicillioides*, *F. curvula*, *Triscelophorus monosporus*, *Clavatospora longibrachiata*, *Articulospora tetracladia*, *Clavariopsis aquatica*, *Lemonniera aquatica*, *Tetracladium marchalianum* and *Lemonniera terrestris* were the ten top-ranking species on the bait leaves in the canal in summer (Table 4).

In a comparison of communities detected on *Salix* leaf baits in different seasons, the autumn community showed a similarity of 84.6% with the winter community, 90.2% with the spring and 87.5% with the summer community on the basis of presence and absence of species. The spring community showed the highest similarity index (93.9%) with the summer community. On the other hand, the winter community had a similarity index of 79.2% with the spring and 72.0% with the summer community (Table 6).

Table 5. Freshwater hyphomycete communities colonizing leaf baits of *Salix babylonica* submerged in the Jabori Canal over four different seasons. Acronyms used in Fig. 1 are also given. RF = relative frequency.

| | Autumn | | Winter | | Spring | | Summer | |
|---|---|---|---|---|---|---|---|---|
| | RF | $(p_1)(\log_2 p_1)$ | RF | $(p_1)(\log_2 p_1)$ | RF | $(p_1)(\log_2 p_1)$ | RF | $(p_1)(\log_2 p_1)$ |
| Aa: *Alatospora acuminata* Ingold | 0.0843 | – 0.0905 | 0.0740 | – 0.0836 | 0.0405 | – 0.0563 | 0.0314 | – 0.0471 |
| *A. constricta* Dyko | 0.0248 | – 0.0398 | 0.0184 | – 0.0319 | – | – | – | – |
| *Anguillospora crassa* Ingold | 0.0248 | – 0.0398 | – | – | 0.0101 | – 0.0201 | 0.0262 | – 0.0414 |
| Al: *A. longissima* (de Wild.) Ingold | 0.0694 | – 0.0808 | 0.0509 | – 0.0658 | 0.0760 | – 0.0850 | 0.0454 | – 0.0609 |
| *Articulospora proliferata* Jooste, Roldan & Merwe | 0.0248 | – 0.0398 | 0.0138 | – 0.0256 | 0.0202 | – 0.0342 | 0.0314 | – 0.0471 |
| At: *A. tetracladia* Ingold | 0.0611 | – 0.0741 | 0.0555 | – 0.0696 | 0.0506 | – 0.0655 | 0.0577 | – 0.0714 |
| *Bacillispora aquatica* Nilsson | 0.0197 | – 0.0335 | 0.0138 | – 0.0256 | 0.0101 | – 0.0201 | 0.0157 | – 0.0283 |
| *B. inflata* Iqbal & Bhatty | 0.0148 | – 0.0270 | 0.0138 | – 0.0256 | 0.0202 | – 0.0342 | 0.0105 | – 0.0207 |
| Ca: *Clavariopsis aquatica* de Wild. | 0.0594 | – 0.0728 | 0.0648 | – 0.0770 | 0.0608 | – 0.0739 | 0.0577 | – 0.0714 |
| *C. azlanii* Nawawi | – | – | – | – | 0.0152 | – 0.0276 | 0.0314 | – 0.0471 |
| Cl: *Clavatospora longibrachiata* (Ingold) Nilsson ex Marvanová & Nilsson | 0.0478 | – 0.0631 | 0.0555 | – 0.0696 | 0.0557 | – 0.0698 | 0.0612 | – 0.0742 |
| *Dactylella aquatica* (Ingold) Ranzoni | 0.0148 | – 0.0270 | 0.0138 | – 0.0256 | 0.0050 | – 0.0115 | 0.0105 | – 0.0207 |
| *Dimorphospora foliicola* Tubaki | 0.0248 | – 0.0398 | 0.0231 | – 0.0378 | 0.0202 | – 0.0342 | 0.0314 | – 0.0471 |
| Fc: *Flagellospora curvula* Ingold | 0.0941 | – 0.0965 | 0.0833 | – 0.0899 | 0.0810 | – 0.0884 | 0.0734 | – 0.0832 |
| *F. fusarioides* Iqbal | 0.0297 | – 0.0453 | 0.0323 | – 0.0481 | 0.0152 | – 0.0276 | 0.0366 | – 0.0525 |
| Fp: *F. penicillioides* Ingold | – | – | – | – | 0.0591 | – 0.0725 | 0.0786 | – 0.0868 |
| *F. stricta* Nilsson | – | – | 0.0093 | – 0.0188 | – | – | – | – |
| Gi: *Geniculospora inflata* (Ingold) Nilsson ex Marvanová & Nilsson | 0.0446 | – 0.0602 | 0.0462 | – 0.0616 | 0.0405 | – 0.0563 | 0.0314 | – 0.0471 |
| *Heliscus lugdunensis* Sacc. & Therry | 0.0197 | – 0.0335 | 0.0323 | – 0.0481 | 0.0304 | – 0.0461 | 0.0366 | – 0.0525 |
| La: *Lemonniera aquatica* de Wild. | 0.0643 | – 0.0766 | 0.0694 | – 0.0804 | 0.0658 | – 0.0777 | 0.0541 | – 0.0685 |
| *L. centrosphaera* Marvanová | 0.0346 | – 0.0505 | 0.0277 | – 0.0431 | 0.0202 | – 0.0342 | – | – |
| *L. filiformis* Petersen ex Dyko | 0.0248 | – 0.0398 | 0.0231 | – 0.0378 | – | – | – | – |
| Lt: *L. terrestris* Tubaki | 0.0397 | – 0.0556 | 0.0648 | – 0.0770 | 0.0456 | – 0.0611 | 0.0471 | – 0.0625 |
| Lc: *Lunulospora curvula* Ingold | 0.0397 | – 0.0556 | – | – | 0.0709 | – 0.0814 | 0.0892 | – 0.0936 |
| *Margaritispora aquatica* Ingold | 0.0148 | – 0.0270 | 0.0231 | – 0.0378 | 0.0101 | – 0.0201 | 0.0262 | – 0.0414 |
| *Mycocentrospora clavata* Iqbal | – | – | 0.0093 | – 0.0188 | – | – | – | – |
| Tm: *Tetracladium marchalianum* de Wild. | 0.0545 | – 0.0688 | 0.0555 | – 0.0696 | 0.0489 | – 0.0640 | 0.0523 | – 0.0670 |
| *Tricladium attenuatum* Iqbal | – | – | 0.0184 | – 0.0319 | 0.0152 | – 0.0276 | – | – |
| Tc: *T. chaetocladium* Ingold | 0.0429 | – 0.0586 | 0.0601 | – 0.0733 | 0.0405 | – 0.0563 | – | – |
| *T. splendens* Ingold | – | – | 0.0231 | – 0.0378 | – | – | – | – |
| Ts: *Triscelophorus monosporus* Ingold | 0.0248 | – 0.0398 | – | – | 0.0405 | – 0.0563 | 0.0629 | – 0.0755 |
| *Varicosporium elodeae* Kegel | – | – | 0.0093 | – 0.0188 | – | – | – | – |
| ∑ Frequencies | 672.4 | | 720.1 | | 657.8 | | 635.6 | |
| Number of species | 25 | | 27 | | 26 | | 23 | |
| *H*-diversity | | 4.4246 | | 4.3362 | | 4.3292 | | 4.4677 |
| *E* (Evenness) | | 0.9527 | | 0.9119 | | 0.9211 | | 0.9876 |

When the relative frequencies of occurrence are taken into account, the similarity index between the winter and summer communities decreased to 66.3 (Table 6). This is at least partly due to the change in deciduous substratum available in the summer.

## DISCUSSION

Fourteen species dominated the four freshwater hyphomycete assemblages in four seasons. *Triscelophorus monosporus*, *Flagellospora penicillioides* and *Lunulospora curvula* disappeared in winter. The other eleven species were essentially the most frequent fungi all year round (Fig. 2). The seasonal differences were caused by 1) a shift in the relative frequency of a few dominant species such as *Articulospora tetracladia*, *Alatospora acuminata*, *Lemonniera aquatica* and *L. terrestris* in ten top-ranking species of a community of each season, 2) the dominance of temperate species (*Tricladium chaetocladium*) in winter/cold months or tropical species (*Lunulospora curvula*, *Triscelophorus monosporus* and *Flagellospora penicillioides*) in summer or warm months, 3) the concentration of some less abundant species (*Geniculospora inflata*) in spring (Fig. 2), and 4) the changing degradation rates of leaf baits over the year (summer > spring > autumn > winter). This factor influenced the residence period of the *Salix* leaf baits and the period a community took to develop. A freshwater hyphomycete community took 6 weeks to develop in winter, 4 weeks in spring, summer and autumn (Fig. 2).

The seasonal pattern of summer assemblage with typical warm water species, e.g. *Lunulospora curvula*, *Triscelophorus monosporus* and *Flagellospora penicillioides* in the Jabori Canal is similar to that in several streams, in England (Iqbal & Webster 1973b), in Augusta Creek, Michigan (Suberkropp 1984), in South Western France (Chauvet 1991), and in the River Teign, England (Bärlocher 1991).

Freshwater hyphomycete communities of autumn, winter and spring on the leaves were dominated by *Flagellospora curvula* and the community of summer was dominated by *Lunulospora curvula*. Nine out of the ten top-ranking species in the autumn and winter were identical but differed in their ranking. *Lemonniera terrestris* was among the ten top-ranking species in the winter community and *Geniculospora inflata* in the autumn community.

Freshwater hyphomycete communities on the leaves of *Salix babylonica* submerged in the Jabori Canal in winter and summer showed a similarity index of 72.0 on the basis of presence and absence of species (Table 6). This similarity index dropped to 66.3% (the lowest value among 4 communities of the 4 different seasons) when relative frequencies of individual species were considered (Table 6). This high dissimilarity coefficient (33.7%) can be attributed to seasonal differences in temperature which affects a shift in the relative abundance of some abundant/dominant species e.g., *Lunulospora curvula*, *Triscelophorus monosporus* and *Flagellospora penicillioides*. Abundance of *L. curvula,* coinciding with the leaf fall and warm temperature of autumn, and *Tricladium chaetocladium* in winter in several streams in England was reported by Iqbal and Webster (1973b). Suberkropp (1984) reported *L. curvula* and *T. chaetocladium* in summer and winter, respectively, in Augusta Creek. The absence of this group of warm temperature species (*L. curvula, F. penicillioides* and *T. monosporus*) in winter and the less commonly occurring winter group e.g., *T. chaetocladium* in warmer months, can be connected with their growth responses to temperature in laboratory experiments (Webster *et al.* 1976).

Table 6. Similarity comparisons of the fungal communities colonizing *Salix* leaf baits in 4 seasons in the Jabori Canal.

| | Autumn | Winter | Spring | Summer |
|---|---|---|---|---|
| Autumn | – | 84.6 (79.4) | 90.2 (78.8) | 87.5 (72.0) |
| | Winter | – | 79.2 (73.5) | 72.0 (66.3) |
| | | Spring | – | 93.9 (81.2) |

Upper numbers: Sørensen's similarity index (%) calculated as the number of common species found in two communities divided by the average number of species in both. Lower numbers (in parentheses): The second index calculated from the sum of lower occurrence percentages of species in either of the communities.

Higher similarity indices among the fungal communities of the four seasons are indicators of greater homogeneity. A greater homogeneity in fungal species composition in a community may be achieved with greater environmental stability. This may include regular deposition of deciduous substratum (deciduous leaves), seasonal addition of agricultural products such as wheat and rice straw and enrichment of the canal water with higher amounts of nitrates and phosphates which would stimulate fungal activity, resulting in higher colonization rates and number of conidia/mg, and accelerated mass loss of leaf baits.

These higher similarity indices are accompanied with a close range of species diversity *H* values of 4.329–4.4646. Freshwater hyphomycete communities in the Jabori Canal are dominated by winter species such as *Flagellospora curvula*, *Lemonniera aquatica*, *L. terrestris*, *Alatospora acuminata*, *Tricladium chaetocladium*, *Articulospora tetracladia*, *Clavatospora longibrachiata*, *Tetracladium marchalianum* and *Anguillospora longissima*. This assemblage of freshwater hyphomycetes dominated the autumn community with minor adjustments in the ranking of top-ranking species. In the spring, *Lunulospora curvula* and *Flagellospora penecillioides* joined the group of ten top-ranking species. *Tricladium chaetocladium* and *Lemonniera terrestris* occurred with lower frequency. Similarly, in the summer *Lunulospora curvula*, *Flagellospora penicillioides* and *Triscelophorus monosporus* were abundant and *Tricladium chaetocladium*, *Articulospora tetracladia* and *Alatospora acuminata* occurred less frequently.

*Lunulospora curvula* and *Flagellospora penicillioides* in spring and summer and *Triscelophorus monosporus* in summer caused a change in ranking of the ten top-ranking species of the temperate region. This did not affect the species diversity value (*H*), yet these changes caused by replacements by the tropical species indicates significant environmental modification during the transition from winter to summer conditions. This change brought about by the addition of summer species created a greater evenness (*E*) in the summer (0.9876) than in the winter community (0.9527) (Table 5).

In the canal, the annual temperature range was much smaller (Fig. 1) than in the River Teign (Shearer & Webster 1985), the River Exe (Iqbal & Webster 1973b), Augusta Creek (Suberkropp 1984), or streams in south western France (Chauvet 1991). It was similar to the range in the Touyer (Gessner *et al*. 1993). However, in the Touyer, the warm water species did not appear in the summer since the temperature never reached 16–18°C (Gessner *et al*. 1993). The increase in frequency of occurrence of warm temperature species (*Lunulospora curvula*, *Flagellospora penicillioides* and *Triscelophorus monosporus*) in the Jabori Canal is not related with the establishment of the temperature regime in summer as postulated by the temperature threshold hypothesis.

The shift in community structure in the present studies was not accompanied by species extinction as is the case with succession of saprophytic organisms (Frankland 1981, Swift 1981). Distinct species replacements were not observed on leaves, rather the initial colonizers persisted as the new colonizer species were added and all these members of the community disappeared as the substratum was degraded (see Chamier & Dixon 1982, Bärlocher & Schweizer 1983, Shearer & Webster 1991).

Temperature influenced the colonization of the bait leaves by the freshwater hyphomycetes by affecting the rate of degradation (Table 6). Degradation was faster in summer than in other seasons (Suberkropp 1984, Gessner *et al*. 1993). The rapid degradation of the bait leaves in the Jabori Canal is accompanied by a rapid development of a community of freshwater hyphomycetes on the leaf baits. Six (in winter) to 20 (in summer) species colonized the bait leaves as pioneer species, in the first week of immersion (Table 6). Temperature also affected the time period taken by a species to reach its peak frequency of occurrence and the community to develop on the leaves. Communities were saturated with species after 3 weeks in autumn and winter, and after 2 weeks in spring and summer (Fig. 2).

A summer community with more than 10 frequently occurring species coincided with 70% loss in leaf mass after 4 weeks. An impoverished community of these fungi was represented by *Articulospora tetracladia*, *Clavatospora longissima*, *Flagellospora curvula*, *Tetracladium marchalianum* and *Tricladium chaetocladium* etc., colonizing mostly the mid rib, veins and other lignified leaf tissues.

These differences in the development of fungal communities on the leaves, such as number of species and the dynamics of conidia, are correlated with rate of leaf breakdown (Gessner *et al.* 1993, Iqbal 1994). The tight coupling of community development with the dynamics of leaf mass loss is indicative of a close correlation between a characteristic fungal assemblage and the state of leaf decay (Chamier & Dixon 1982, Gessner *et al.* 1993).

Typical winter species such as *Alatospora acuminata* and *Anguillospora longissima,* and summer species *Lunulospora curvula* and *Triscelophorus monosporus,* took 3 weeks to peak in spring and summer while these communities developed after 4 weeks in winter and summer (Table 3). These winter species reached their peak along with the community in winter (November–December) and autumn (October–November). The higher number of species in the winter community is indicative of the availability of a complex food web (see Pielou 1977) due to the pulsed deposition of leaf litter (Fig. 3). In winter the available substratum and suitable temperature which are two important factors regulating the abundance of species and maximal sporulation of these fungi cannot be separated. An increase in conidial numbers coinciding with leaf fall has been reported by Iqbal and Webster (1973b), but an increase in number of species cannot be attributed to leaf litter deposition alone. *Alatospora acuminata* and *Anguillospora longissima,* being winter species, take longer to reach their peak than *Lunulospora curvula* and *Triscelophorus monosporus* which reach their peaks quickly. On the other hand, *Lemonniera terrestris* took 5 weeks to reach its peak in autumn while the community developed in 4 weeks (Fig. 2). Obviously, the narrow annual temperature range brings these winter and summer species together in the same community.

The species richness of the Jabori Canal may be due to the presence of higher amounts of nitrates and phosphates, a rich riparian vegetation and seasonal addition of agricultural products such as wheat and rice straw and leaves of other crops in the canal water. Gunasekera *et al.* (1983) reported higher mass losses and greater fungal (freshwater hyphomycetes) activity on submerged blocks using ecologically improbable levels of nitrates and phosphates. The faster rate of mass losses of *Salix* leaf baits in the canal, accompanied by rapid fungal colonization is in line with the findings of Gunasekera *et al.* (1983) and Suberkropp (1991).

There was no correlation between the number of conidia of species in the canal water and the degree of its colonization on *Salix* leaf baits (Tables 2–5). Species with conventional conidia such as *Heliscus lugdunensis*, *Dactylella aquatica* (mostly), *Mycocentrospora clavata* and *Flagellospora fusarioides* (at times), which were present among the ten top-ranking species in fungal communities detected in the canal water, occurred with low frequencies on the *Salix* leaf baits. Several species with tetraradiate conidia e.g., *Articulospora tetracladia*, *Lemonniera terrestris*, *Clavatospora longibrachiata* etc., which were present in low numbers in the canal were among the ten top-ranking species on the leaf baits. Chamier and Dixon (1982), Sanders and Anderson (1979), Shearer and Webster (1985c) and Iqbal (1994) also found large discrepancies for individual freshwater hyphomycete species between the number of conidia/l available for colonization and the actual fruiting pattern on leaf baits.

The composition of the conidia of different species is represented by the species composition of the community worked out but by the filtration method of Iqbal and Webster (1973b) and Iqbal (1994). The dominant (the ten top-ranking) species of this conidial pool may not be the same as those on the leaf baits. All the conidia in the pool may not anchor on the submerged substrata. Different conidia are trapped on substrates (Webster 1959) and by air bubbles selectively (Iqbal & Webster 1973a, Iqbal 1993, 1994). Incidently conidia which anchor more efficiently on submerged substrata are also caught up in foam more efficiently.

Conidia trapped in foam concentrate thus represent proportionately the numerical strength of the inoculum potential. Not all conidia anchoring on the submerged leaves are viable. The temperature of the canal water and the residence period of a conidium in water will influence its viability (Iqbal & Webster 1973a, Sridhar & Bärlocher, unpublished data) and the presence of inhibitors in submerged material may also affect the colonization (Gunasekara *et al.* 1983). Freshwater hyphomycete communities detected on submerged bait leaves are thus the outcome of successful colonization by viable conidia. This may explain the discrepancy between the species composition of communities detected on leaves and those trapped in foam concentrate.

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