Open Archive TOULOUSE Archive Ouverte (OATAO)
OATAO is an open access repository that collects the work of Toulouse researchers and makes it freely available over the web where possible.

This is an author-deposited version published in : http://oatao.univ-toulouse.fr/
Eprints ID : 9633

To link to this article : DOI :10.1016/S0953-7562(09)80238-4
URL : http://dx.doi.org/10.1016/S0953-7562(09)80238-4

To cite this version : Gessner, Mark O. and Thomas, Marielle and Jean-Louis, Anne-Marie and Chauvet, Eric *Stable successional patterns of aquatic hyphomycetes on leaves decaying in a summer cool stream.* (1993) Mycological Research, vol. 97 (n° 2). pp. 163-172. ISSN 0953-7562

Any correspondance concerning this service should be sent to the repository administrator: staff-oatao@listes-diff.inp-toulouse.fr

Stable successional patterns of aquatic hyphomycetes on leaves decaying in a summer cool stream

MARK O. GESSNER*, MARIELLE THOMAS†, ANNE-MARIE JEAN-LOUIS AND ERIC CHAUVET

Centre d'Ecologie des Ressources Renouvelables, CNRS, 29, rue Jeanne Marvig, 31055 Toulouse Cédex, France

The colonization of leaf litter (*Alnus glutinosa*) by aquatic hyphomycetes was studied in a summer cool stream of the French Pyrenees. In spite of the rapid decomposition of leaves, the fungal community exhibited a characteristic successional pattern with three phases. The initial colonization stage was defined by a dense sporulation of the five species *Tetrachaetum elegans, Lemonniera aquatica, L. centrosphaera, L. terrestris,* and in particular *Flagellospora curvula*. After four weeks of colonization, a mature community had established. It was characterized by high species diversity and peak fungal biomass, which was measured as ergosterol content, and coincided with about 50% loss in leaf mass. With leaf decay progressing further, diversity diminished concomitant with a slight reduction in fungal biomass and a sharp decrease in the rate of conidial production. Typical species of this late successional stage were *Clavatospora longibrachiata, Heliscella stellata* and *Goniopila monticola*. This successional pattern proved to be stable both within the period of leaf fall in one year and between two successive years. Between-seasons differences were quite small as well, the striking lack of species replacement apparently being due to not exceeding the threshold temperature of 16–18 °C as previously defined in literature. In spite of this general stability in community structure, correspondence analysis discriminated the communities on leaf packs with equal exposure times according to season, with the cyclical arrangement of leaf packs on the principal factorial plane reflecting the seasonal cycle. The colonization of fresh (non-dried) leaf litter by aquatic hyphomycetes was delayed compared to air-dried litter; however, the lead diminished with progressing leaf decay, resulting in nearly identical communities on fresh and dried leaves after four weeks of decomposition.

Since the discovery of a unique fungal flora associated with decaying leaf litter in streams and rivers, a considerable body of literature has accumulated on the ecology of these fungi that Ingold (1942) has termed aquatic hyphomycetes and that are now sometimes referred to as Ingoldian fungi (Bärlocher, 1982). A number of studies have dealt with the seasonal dynamics of aquatic hyphomycetes by examining the composition of conidia in foam (Chauvet, 1992), in river water (Shearer & Webster, 1985*a*; Thomas, Chilvers & Norris, 1991), or on decaying leaves that were randomly picked from the stream bed (Shearer & Lane, 1983; Shearer & Webster, 1985*a*; Chauvet, 1992). In other investigations, leaf litter was introduced to streams experimentally so as to study the colonization patterns of aquatic hyphomycetes on their natural substrate (e.g. Bärlocher & Kendrick, 1974; Suberkropp & Klug, 1976; Chamier & Dixon, 1982; Chergui & Pattee, 1988).

Foam sampling and membrane filtration of river water are inappropriate to assess the fungal assemblages associated with leaf litter, because these methods reflect the production of conidia on various substrates and are also selective (Shearer & Lane, 1983; Shearer & Webster, 1985*b*). Analysing the mycoflora on leaves naturally deposited in the stream channel is only a partial remedy for these shortcomings because the residence time of this material is not precisely known. Furthermore, due to the pulsed input of leaves to temperate streams and the marked differences in breakdown rates among leaf species (Webster & Benfield, 1986), plant material available

Table 1. Water-chemical characteristics of the Touyre during field experiments (TDP = total dissolved phosphorus, DOC = dissolved organic carbon)

	Oct. 1988 to Feb. 1989		Nov. 1989 to Sep. 1990	
Parameter	Mean	Range	Mean	Range
pH	6·8	6·7–7·0	7·5	6·5–8·1
Alkalinity (meq. l^{-1})	0·24	0·22–0·26	0·41	0·17–0·78
Spec. cond. ($\mu S\ cm^{-1}$, 25°)	46	44–48	57	35–113
Ca^{2+} (mg l^{-1})	4·9	4·6–5·1	7·9	4·5–16·2
Mg^{2+} (mg l^{-1})	0·56	0·54–0·58	0·52	0·34–1·02
NO_3^--N (mg l^{-1})	0·13	0·09–0·20	0·22	0·12–0·28[a]
PO_4^{3-}-P ($\mu g\ l^{-1}$)	< 2			< 2–9
TDP ($\mu g\ l^{-1}$)	< 2			< 2–13
DOC (mg l^{-1})	0·9	0·7–1·4		

[a] 1·04 mg l^{-1} on 3 Aug. 1990.

* Corresponding author, current address: Projektzentrum Ökosystemforschung, Christian-Albrechts-Universität, Schauenburger Str. 112, 2300 Kiel 1, Germany.

† Current address: Laboratoire de Biologie Appliquée, 34 rue Sainte-Catherine, 54000 Nancy, France.

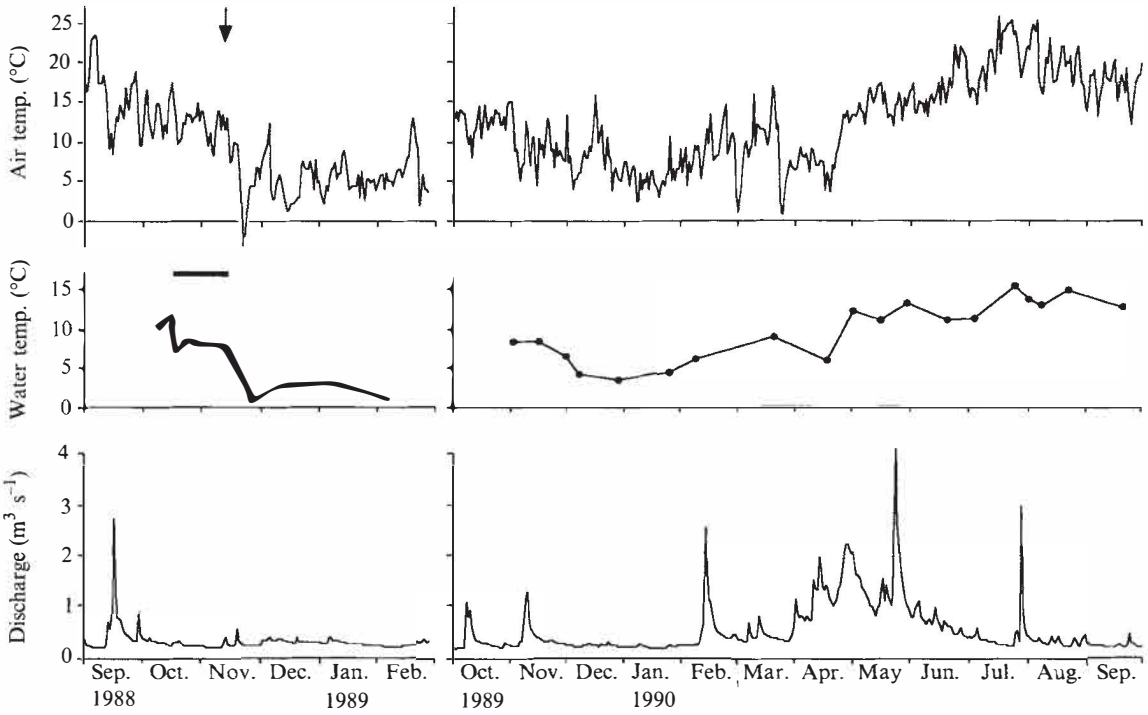

Fig. 1. Air temperature at 5 km distance from the study sites (650 m elevation), water temperature and discharge of the Touyre. Discharge values are corrected daily means recorded at a gauging station 3 km downstream from the study sites. The arrow represents the exposure date of the November series and the horizontal bar the period of bulk leaf fall.

for sampling at different periods of the year differs in age and quality. Seasonal differences in fungal community structure emerging from the examination of such samples are therefore either due to fungal succession as a result of changing substrate quality (internal factors) or to differences in general environmental conditions such as temperature, inoculum potential, and activity of detritivorous arthropods (external factors). The final outcome is probably the result of both processes, one superimposed on the other.

The discrimination of these factors is possible using an experimental approach. Consequently, Suberkropp (1984) and Gönczöl (1989) analysed communities of aquatic hyphomycetes developing on standardized leaf packs exposed in streams at different periods of the year. However, decay rates and successional speed vary with season (Suberkropp, 1984), so different successional stages can still be recorded even if identical exposure times are chosen. In the present study, standardized leaf packs were thus not only exposed at different seasons of the year but also retrieved at repeated intervals. The specific aims of the investigation were (1) to characterize the autumnal colonization pattern of aquatic hyphomycetes on alder leaves decomposing in a cold-water low-nutrient stream, (2) to check whether these patterns are stable within the period of natural leaf fall, (3) to document variations over the annual cycle, and (4) to elucidate differences between the colonization of naturally fallen fresh and air-dried leaves. As the spatial distribution of aquatic hyphomycetes on leaf litter is patchy (Shearer & Lane, 1983; Chamier, Dixon & Archer, 1984), care was taken to base conclusions on an extensive set of data (Table 2).

STUDY SITE

The colonization of leaf litter by aquatic hyphomycetes was studied in the Touyre, a low-nutrient soft-water stream located in the French Pyrenees (42° 52′ N, 1° 45′ E). The study site chosen in 1988 was at 940 m elevation and corresponds to the one described in Gessner (1991). In the following year, a reach was chosen some 500 m downstream; it has generally similar characteristics but is situated downstream from a small reservoir from where water can be diverted to a hydroelectric power plant. It was thus hoped to protect the introduced leaf packs from major spates, but this turned out to be a fallacy. At the study sites the channel gradient is 5%, average depth is 15–20 cm and stream width 6·5 m and 5 m, respectively. Bed sediments are primarily composed of cobble and boulders, and the riparian vegetation consists mainly of ash (*Fraxinus excelsior* L.), alder (*Alnus glutinosa* (L.) Gaertn.), and beech (*Fagus sylvatica* L.) with an understory of hazel (*Corylus avellana* L.). Further characteristics of the Touyre are given in Fig. 1 and Table 1.

MATERIAL AND METHODS

Standard leaf packs of about 5 g dry mass were constructed from autumn-shed leaves of *Alnus glutinosa* (L.) Gaertn., enclosed in nylon-mesh bags (9 mm openings) supported on a metal frame, attached to house bricks, and submerged in the Touyre (Gessner, 1991). Fresh leaves were immersed within 3 h after collection, while the leaves referred to as air-dried were kept at ambient temperature for at least 1 wk before

Table 2. Overview of the series of leaf packs analysed for fungal community structure after exposure in the Touyre

Date of submersion	Pretreatment of litter	Exposure time (wk)	Leaf discs examined	Name of series
17 Oct. 1988	None	0·4, 1, 2, 4, 6, 8	480	Oct. 1988
17 Oct. 1988	Air-dried	0·4, 1, 2, 4, 6, 8	480	Dry 1988
13 Nov. 1988	None	2, 4, 8	270	Nov. 1988
3 Nov. 1989	None	2, 4, 8	162	Nov. 1989
3 Nov. 1989	Air-dried[a]	2, 4, 8	162	Autumn
26 Jan. 1990	Air-dried[a]	2, 4, 8	162	Winter
4 May 1990	Air-dried[a]	2[b]	54	May
8 Jun. 1990	Air-dried[a]	2, 4[c]	108	Spring
27 Jul. 1990	Air-dried[a]	2, 4[c]	108	Summer

[a] Leaves used in the autumn, winter, May, spring and summer series were collected simultaneously.

[b] The remaining packs were lost during a flood.

[c] After 8 wk, leaf packs were entirely broken down.

Table 3. Aquatic hyphomycete species identified on leaf litter of *Alnus glutinosa* decaying in the Touyre. Acronyms used in Figs 2–6 are also given

AA	*Alatospora acuminata* Ingold
AF	*Alatospora flagellata* (Gönczöl) Marvanová
	Alatospora pulchella Marvanová
	Anguillospora crassa Ingold
AL	*Anguillospora longissima* (Sacc. & Syd.) Ingold
AT	*Articulospora tetracladia* Ingold
	?Calcarispora hiemalis Marvanová & Marvan
CA	*Clavariopsis aquatica* de Wildeman
CL	*Clavatospora longibrachiata* (Ingold) Marvanová & S. Nilsson
CS	*Crucella subtilis* Marvanová
CQ	*Culicidospora aquatica* R. H. Petersen
	Culicidospora gravida R. H. Petersen
	Dendrospora erecta Ingold
	Dendrospora fusca Descals & Webster
DF	*Dimorphospora foliicola* Tubaki
	Flabellospora acuminata Descals
FC	*Flagellospora curvula* Ingold
GI	*Geniculospora inflata* (Ingold) S. Nilsson ex Marvanová & S. Nilsson
GM	*Goniopila monticola* (Dyko) Marvanová & Descals
HS	*Heliscella stellata* (Ingold & Cox) Marvanová & S. Nilsson
	Heliscina antennata Marvanová
	Heliscina campanulata Marvanová
HL	*Heliscus lugdunensis* Saccardo & Thérry
	?Jaculispora submersa Hudson & Ingold
	Lemonniera ?alabamensis Sinclair & Morgan-Jones
LA	*Lemonniera aquatica* de Wildeman
LE	*Lemonniera centrosphaera* Marvanová
LT	*Lemonniera terrestris* Tubaki
	Stenocladiella neglecta (Marvanová & Descals) Marvanová & Descals
	Sympocladium frondosum Descals
TG	*Taeniospora gracilis* var. *gracilis* Marvanová
TE	*Tetrachaetum elegans* Ingold
TM	*Tetracladium marchalianum* de Wildeman
	Tetracladium maxilliforme (Rostrup) Ingold
	Tetracladium setigerum (Grove) Ingold
	?Tricladium chaetocladium Ingold
TP	*Tricladium patulum* Marvanová & Marvan
TL	*Tricladium splendens* Ingold
	Tripospermum camelopardus Ingold, Dann & McDougall
	Tripospermum myrti (Lind.) Hughes
TU	*Tumularia aquatica* (Ingold) Descals & Marvanová
	Tumularia tuberculata (Gönczöl) Descals & Marvanová
	Varicosporium elodeae Kegel

submersion. From October 1988 to August 1990 a total of 99 packs, divided into 9 series, were placed in the stream, and these were later retrieved at intervals of 4 wk or less (Table 2). At each sampling date, three replicate packs were removed, placed in plastic containers that were partially filled with stream water, and returned to the laboratory on ice. On arrival, individual leaves were carefully rinsed, and three leaves per pack were taken for the analysis of fungal community structure. When leaves occurred in distinct layers within the pack, one leaf each from the upper, middle and lower third was chosen so as to obtain a representative cross-section of the fungal colonization of the entire pack.

From each leaf, ten (1988) or six (1989 and 1990) leaf discs were cut out with a cork borer (7 mm diam.) while avoiding major veins. Leaf discs were incubated in uncovered Petri dishes containing 10 ml of filtered stream water for 3 d at 10 °C, fixed in lactophenol (Suberkropp & Klug, 1976; Shearer & Webster, 1985*a*), mounted on slides, stained with about 0·01% trypan blue in lactic acid, and then one half of the disc surface was scanned at a magnification of 200×. Loose conidia and those attached to conidiophores were recorded separately, but for statistical analyses all data were lumped together. Except for the 1988 samples, the total number of spores produced per mm^2 of leaf surface was estimated by counting conidia in 5 microscopic fields (1·27 mm^2 each). Relative abundance of aquatic hyphomycete species was estimated in 8 classes: 0 (0%), 1 (0–1%), 2 (1–5%), 3 (5–20%), 4 (20–40%), 5 (40–60%), 6 (60–80%), 7 (80–100%). Results are either reported as mean abundance index according to the assignment to these categories or as relative frequency, which is the percentage of leaf discs per leaf pack on which a given species was recorded. Because *Alatospora acuminata* and *Stenocladiella neglecta* were not systematically distinguished, they are treated as a single species, and this is referred to as *A. acuminata*. Notice, however, that both species were quite common. Likewise, *L. aquatica* and a form resembling *L. alabamensis* were grouped as *L. aquatica*.

Correspondence analysis (Greenacre, 1984; Chauvet, 1991) was used to detect regular structures in the data set and to display them graphically. The basic idea underlying this multivariate statistical method is to represent the complex information contained in the rows and columns of a data matrix in a set of simple graphical displays while losing a minimum of information. This is achieved by transforming the original variables to a set of abstract 'factors' such that the first few of these account for most of the information present in the original variables. These factors can be visualized as axes in a multidimensional space, and graphical representation of the original variables is then achieved by calculating their co-ordinates in this space and projecting the resulting set of points on a 'factorial' plane defined by two selected axes. Two parameters are important for the interpretation of these displays: the cos^2 of a projected point is a measure of the quality of its representation, and a parameter termed 'inertia' provides information on how much of the variability in the

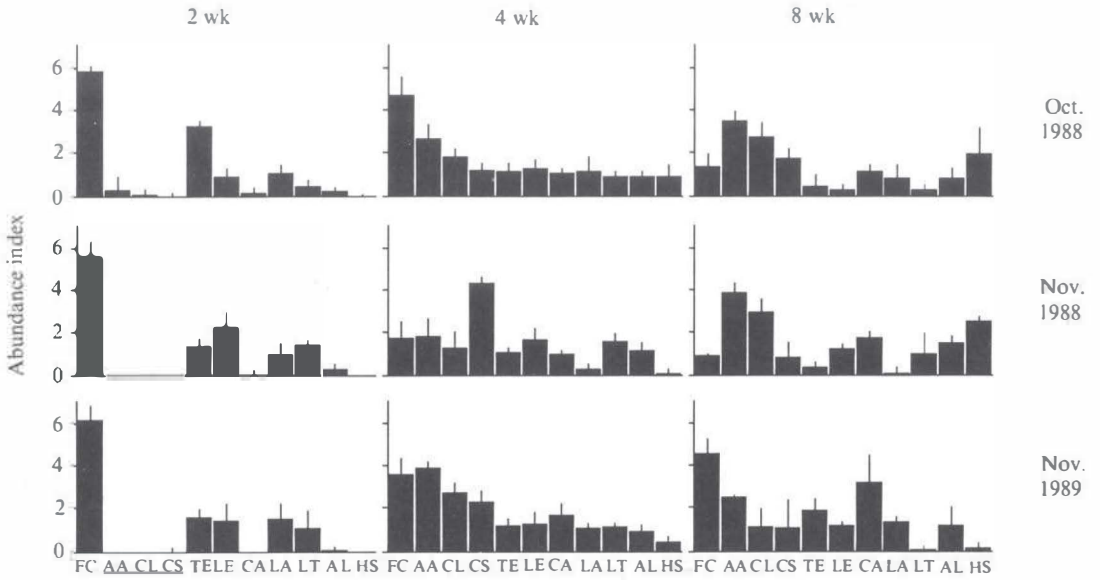

Fig. 2. Autumnal colonization patterns of dominant aquatic hyphomycetes on fresh alder leaves submerged in the Touyre for 2, 4 or 8 wk. Species are ranked on the abscissa according to their importance in the whole data set. Vertical bars denote 1 S.D. For acronyms of species names see Table 3.

data set is accounted for by a given axis. In contrast to related multivariate techniques such as principal component analysis, correspondence analysis treats the rows and the columns of the data matrix in the same way. These may therefore be depicted in the same display and thus be directly compared. All statistical calculations were performed on the basis of the leaf pack as the elemental unit, because only these are both randomly distributed, independent samples (Hurlbert, 1984) and meaningful resource units (*sensu* Swift, 1983). Species occurring only sporadically were excluded from the analysis.

The leaf material not used for the analysis of fungal community structure was frozen, lyophilized, weighed to the nearest 0·01 g, ground to pass a 1 mm-mesh screen, and extracted for ergosterol so as to determine leaf mass loss and leaf-associated fungal biomass (Newell, 1992; Gessner & Schwoerbel, 1991). Ergosterol was extracted by homogenization in methanol and quantified using hplc with uv-detection at 280 nm (Gessner, Bauchrowitz & Escautier, 1991).

RESULTS

Colonization patterns in autumn

A complete list of the aquatic hyphomycetes identified in the present study is given in Table 3; additional information on the fungal flora in the Touyre can be found in Chauvet (1992) and Descals & Chauvet (1992).

Figure 2 shows the autumnal colonization pattern of the dominant species on fresh alder leaves. After 3 and 7 days of stream incubation, the production of conidia on leaf litter was only scarcely recorded. The early stage of colonization (2-wk exposure) was characterized by a dense sporulation of *Flagellospora curvula* and the regular occurrence of four other species, namely *Lemonniera aquatica*, *L. centrosphaera*, *L. terrestris* and *Tetrachaetum elegans*. These five fungi remained important components of the community in later stages of decay; however, by day 28 additional species had assumed significant importance, so that at this point in time the community included 13 abundant species (relative frequency > 10%). About 50% of the leaf material was broken down at this stage (Gessner, 1991). After 8 wk, when leaves were substantially degraded and sporulation markedly reduced (Tables 4 and 5), some of these 13 species assumed greater importance while others declined in relative abundance (Fig. 2).

These dynamics of the aquatic hyphomycete community on leaf litter are confirmed by the display of correspondence analysis presented in Fig. 3. With a percentage of 71% inertia ('variance') the principal factorial plane explains more than two-thirds of the total variability inherent in the data set, and the first axis (F1), which explains 57% of inertia alone, opposes the early (2 wk) and the late stages (6 and 8 wk) of colonization. Although the 4-wk samples are poorly represented on the first axis ($\cos^2 < 0{\cdot}25$), they lie systematically between the 2-wk and the 6- and 8-wk samples, with the 8-wk sample in 1989 being a minor exception to this rule. Note, however, that this sample is not adequately represented either ($\cos^2 = 0{\cdot}08$). Thus the arrangement of leaf packs along the first axis can be interpreted as succession of the fungal community.

Among the well-represented species ($\cos^2 > 0{\cdot}7$), *A. acuminata* and *Clavatospora longibrachiata* are associated with the late colonization stage, while *F. curvula* and *T. elegans* are related to the early stage of colonization. Moreover, the three *Lemonniera* species, which were identified as early colonizers (Fig. 2), are represented with positive values on the first axis, while the two species appearing only at a well-advanced stage of decay, *H. stellata* and *G. monticola*, are projected near the left margin of the display (Fig. 3). This pattern remains stable, when one or both of the two species contributing over-proportionally to the calculation of axes (*F. curvula* and *A.*

Table 4. Mass loss of leaf litter of *Alnus glutinosa*, fungal biomass as ergosterol content, and conidial production at different seasons of the year. Values are means ± S.D. of three replicate leaf packs

Season	Exposure time (wk)	Dry mass remaining (%)	Ergosterol content (μg g^{-1} leaf mass)	Conidial production (no. mm^{-2} d^{-1})[a]
Autumn	2	65·9 ± 2·3	370 ± 11	68 ± 23
	4	54·9 ± 5·6	573 ± 28	38 ± 2
	8	22·0 ± 9·1	424 ± 33	5 ± 3
Winter	2	75·8 ± 0·5	77 ± 5	8 ± 3
	4	55·4 ± 3·4	301 ± 31	38 ± 18
	8	24·1 ± 20·6	403 ± 99	24 ± 13
Spring	2	52·6 ± 12·9	241 ± 29	56 ± 13
	4	19·9 ± 8·1	508 ± 54	44 ± 22
Summer	2	48·1 ± 8·0	305 ± 30	55 ± 27
	4	20·4 ± 14·0	271 ± 26	11 ± 1

[a] Produced on one face of the leaf discs.

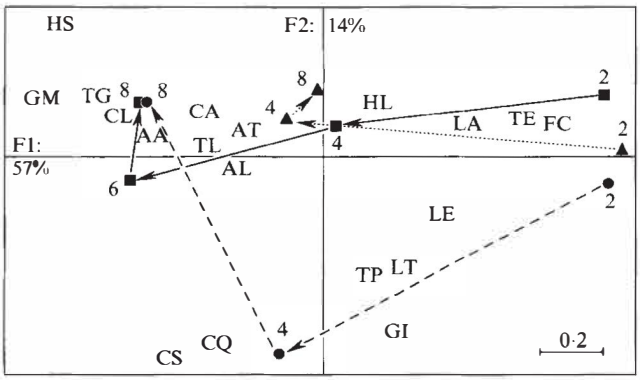

Fig. 3. Projection of the fungal communities associated with leaf packs from October 1988 (■——■), November 1988 (●--●) and November 1989 (▲····▲) on the principal factorial plane of correspondence analysis. Numbers denote the duration of leaf pack exposure in the stream in wk, and arrows indicate the succession of the fungal community. For acronyms of species names see Table 3.

acuminata) are excluded from the analysis. Owing to their inadequate representation ($\cos^2 \ll 0{\cdot}3$), other species such as *Articulospora tetracladia, Culicidospora aquatica, Geniculospora inflata, Heliscus lugdunensis, Tricladium splendens* and *T. patulum* cannot be clearly assigned to a particular successional stage.

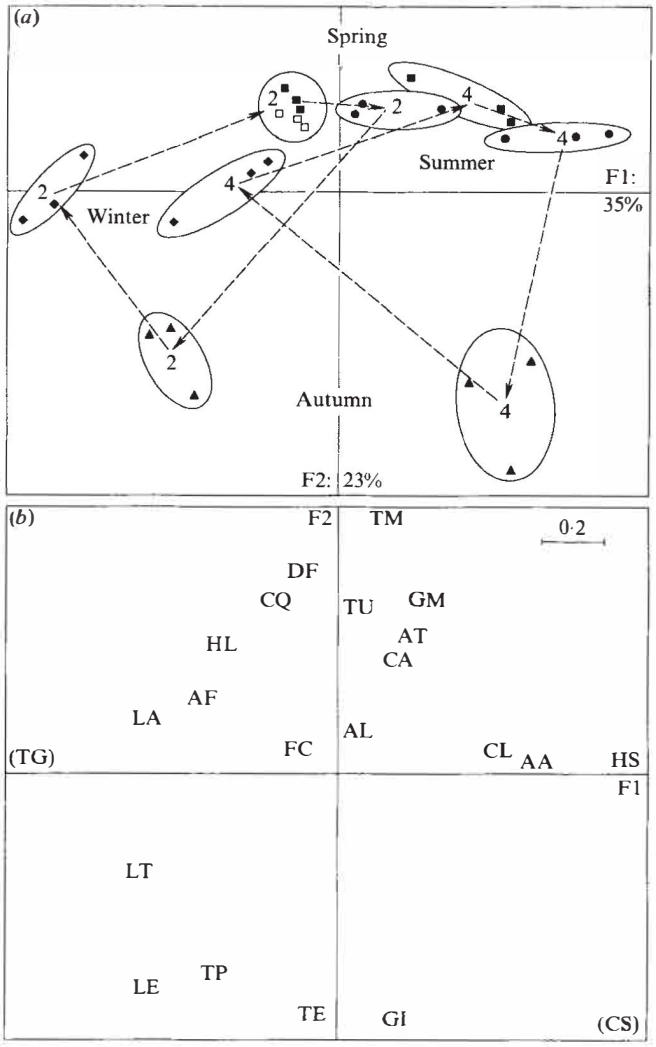

Fig. 4. Projection of aquatic hyphomycete communities on leaf packs (*a*) and leaf-associated hyphomycete species (*b*) of the autumn (▲), winter (◆), May (□), spring (■) and summer (●) series on the principal factorial plane of correspondence analysis. Numbers denote the duration of leaf pack exposure in the stream in wk and arrows indicate the cyclic pattern of seasonal changes. For acronyms of species names see Table 3. *T. gracilis* and *C. subtilis* are located outside the display (−1·6 on F1 and −1·7 on F2, respectively) and therefore appear in parentheses.

Table 5. Fungal biomass as ergosterol content and conidial production of fresh and air-dried leaf litter of *Alnus glutinosa* during decomposition in the Touyre

Pretreatment of leaf litter	Exposure time (wk) 0	0·4	1	2	4	6	8
Ergosterol content (μg g^{-1} detrital dry mass)							
None[a]	4·4	7·9 ± 1·5	14 ± 1	148 ± 1	422 ± 1	462 ± 5	378 ± 9
Air-dried[a]	3·2	14·5 ± 0·4	53 ± 1	229 ± 21	396 ± 32	402 ± 7	366 ± 15
None[b]	0	—	—	271 ± 26	579 ± 20	—	559 ± 22
Air-dried[b]	0	—	—	370 ± 11	573 ± 28	—	424 ± 33
Conidial production (no. mm^{-2} d^{-1})							
None[b]	0	—	—	41 ± 13	54 ± 9	—	11 ± 1
Air-dried[b]	0	—	—	68 ± 23	38 ± 2	—	5 ± 3

[a] Exposure on 17 Oct. 1988, mean ± range (pooled samples).
[b] Exposure on 3 Nov. 1989, mean ± S.D. ($n = 3$).

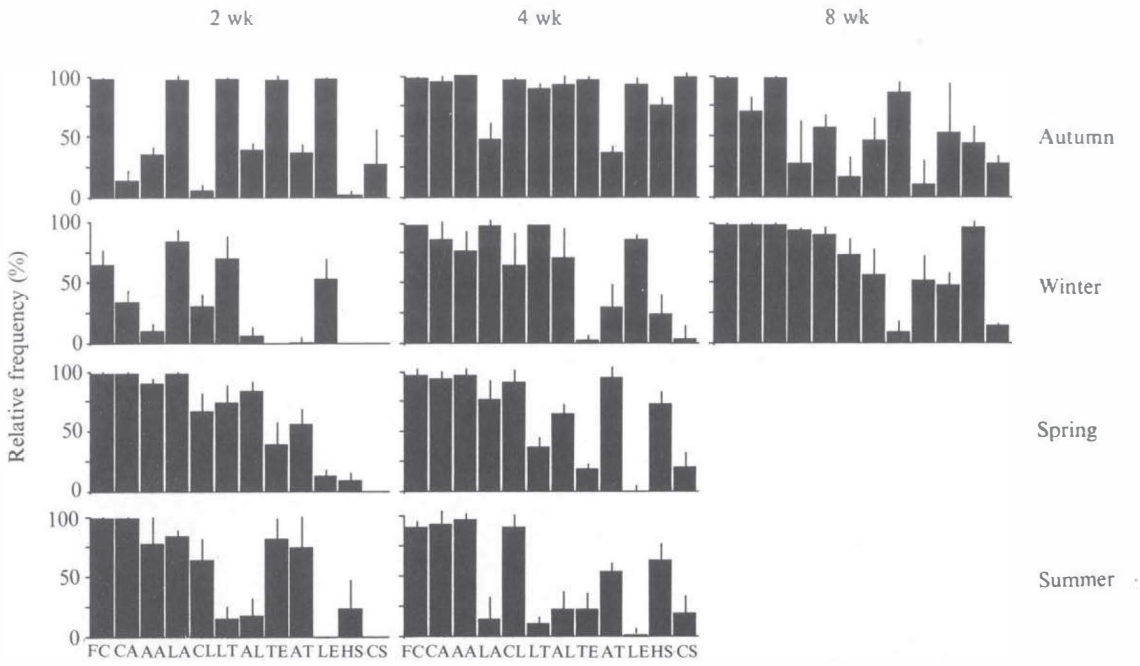

Fig. 5. Seasonal colonization patterns of dominant aquatic hyphomycetes associated with alder leaves in the Touyre. Species are ranked on the abscissa according to their importance in the whole data set. Vertical bars denote 1 S.D. For acronyms of species names see Table 3.

The vertical axis (F2) accounts for 14% of total inertia and resolves differences among the three series October 1988, November 1988 and November 1989 (Fig. 3). These differences are mainly brought about by the 4-wk samples of the November series in 1988, where *C. subtilis* and less so *G. inflata* assume rather great importance to the detriment of *F. curvula*, *A. acuminata* and *C. longibrachiata* (Fig. 2).

Seasonal colonization patterns

In contrast to the great constancy of successional patterns in autumn, there were differences in the colonization of leaf litter among seasons, and these give rise to a cyclic pattern on the principal factorial plane of correspondence analysis (Fig. 4*a*). The first axis contrasts the early stage of colonization in winter ($\cos^2 = 0.54$) and partly in autumn ($\cos^2 = 0{\cdot}33$) with later colonization stages in summer ($\cos^2 = 0{\cdot}71$), spring ($\cos^2 = 0{\cdot}56$), and also partly in autumn ($\cos^2 = 0{\cdot}33$), while the second axis (F2) is essentially defined by the mature (4-wk exposure) autumnal community ($\cos^2 = 0{\cdot}61$). As a result, the fungal assemblages on leaf packs are arranged in two annual cycles (in which the May series integrates perfectly) representing an early and an advanced successional stage, respectively. These cycles are shifted against each other along the first axis, and this shift may be interpreted as reflecting the succession of the fungal community, with the length of the displacement vector being a measure of successional speed. Both the cyclic arrangement of leaf packs and the position of fungal species remain stable when the analysis is performed on the basis of relative frequencies rather than abundance indices.

The cyclic arrangement is not caused by a general replacement of dominant species, because the hyphomycetes classified as abundant in autumn (Fig. 2) were essentially the most frequent fungi all year round (Fig. 5). The seasonal differences are rather due to (1) a shift in the relative abundance of a few dominant species such as *C. aquatica*, *C. subtilis* and *L. centrosphaera* (Figs 2 and 5); (2) the concentration of some less abundant species (notably *Tetracladium marchalianum*) in spring and summer (Fig. 4*b*); and (3) the changing successional speed over the year (summer > spring > autumn > winter). This latter fact resulted in a considerably reduced intensity of colonization in winter after 2 wk of exposure, to communities with similar degrees of maturity in spring after 2 wk, in autumn after 4 wk and in winter after 8 wk, and to an impoverished fungal assemblage in summer after 4 wk of exposure, which would correspond to a much later successional state (> 8 wk) in autumn (Fig. 5).

These differences in the developmental velocity of fungal communities over the year are correlated with the dynamics of fungal biomass, conidial production, and leaf breakdown rates (Table 4).

Colonization of fresh and air-dried leaf litter

Figure 6 shows that aquatic hyphomycetes occupied air-dried leaf litter more rapidly than fresh litter. After one week of stream-exposure, four of the five early colonizers produced conidia on almost half of the air-dried discs, whereas sporulation practically did not occur on fresh leaves. Note, however, that at this time the overall intensity of colonization was low, even on air-dried material. With progressing colonization, differences between the fungal assemblages on fresh and dried litter diminished. After 2 wk, differences in relative frequencies of the early colonizers *F. curvula*, *T. elegans*, *L. centrosphaera* and *L. aquatica* were already small, so

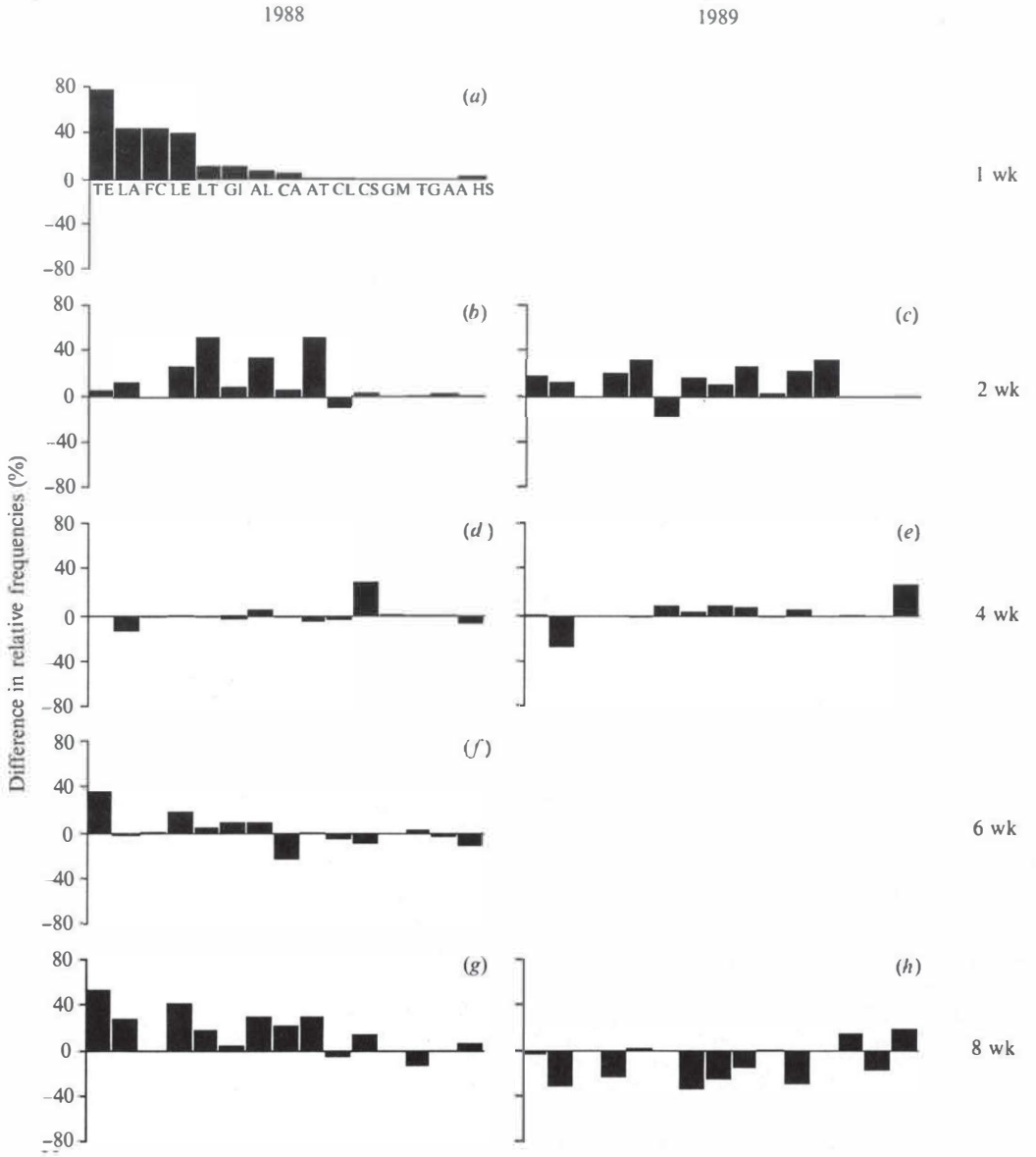

Fig. 6. Differences in relative frequencies of dominant species of aquatic hyphomycetes on fresh and air-dried alder leaves during autumn 1988 and 1989. Positive values indicate higher frequencies on dried litter. For acronyms of species names see Table 3.

communities differed primarily in the abundance of species occurring during later successional stages (Fig. 6*b*, *c*). After 4 wk, then, the initial differences were completely levelled off (Fig. 6*d*, *e*), but subsequently the fungal communities grew apart again, and this occurred in opposite directions in 1988 and 1989 (Fig. 6*f*–*h*). This evolution of aquatic hyphomycete communities on fresh and dried leaf litter apparent in Fig. 6 is in accordance with the dynamics of fungal biomass and conidial production (Table 5).

If the 1988 data are considered separately, correspondence analysis reveals differences between the fungal assemblages on fresh and dried leaves, since the vertical axis (F2) opposes leaf packs according to their pretreatment (Fig. 7*a*). However, this axis only explains 8% of the total variability inherent in the data set, while as much as 67% are accounted for by the first axis (F1) that, as in Fig. 3, represents fungal succession. For the 1989 data, the projection of data points on to the principal factorial plane produces three distinct clusters, and these correspond to the communities on leaf packs submerged for 2, 4 and 8 wk (Fig. 7*b*). Therefore, in contrast to 1988, there was no evidence from the 1989 experiment indicating the development of distinctive fungal communities on fresh and air-dried leaves. This statement holds true also for any other axes of correspondence analysis.

DISCUSSION

Colonization patterns in autumn

The autumnal colonization patterns of aquatic hyphomycetes communities on leaf litter were stable both within the period of natural leaf fall in 1988 (October *v.* November) and between two successive years (1988 *v.* 1989) (Figs 2 and 3). This stability corresponds with the results of Suberkropp

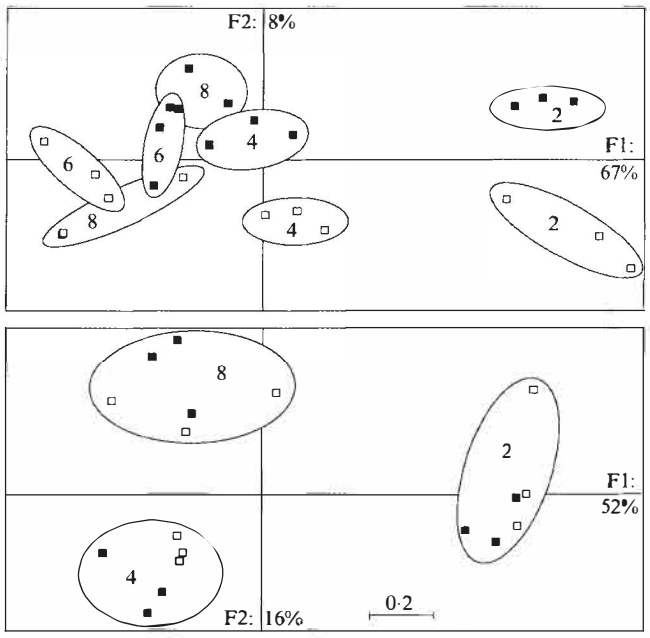

Fig. 7. Projection of fungal communities on fresh (■) and air-dried (□) leaf packs on the principal factorial planes of two separate correspondence analyses performed with data from autumn 1988 (top panel) and autumn 1989 (bottom panel).

(1984) and Suberkropp & Klug (1976), and occurred in spite of the marked decrease in water temperature immediately after exposure of the November series (Fig. 1), and despite the choice of different stream reaches for incubating leaf packs in the two years.

The rapid decomposition of alder leaves in the Touyre (Gessner, 1991; Table 4) did not impede the development of fungal succession on this substrate. This succession was characterized by three stages: an assemblage of five pioneer species in the beginning, a mature community with more than 10 frequent species coinciding with about 50% loss in leaf mass, and an impoverished successional stage defined by a reduced species diversity (Figs 2 and 5), a slightly reduced fungal biomass and a greatly diminished rate of conidial production (Table 4). The tight coupling of community succession with the dynamics of leaf mass loss (Table 4) lends support to the contention of Chamier & Dixon (1982) that for a given habitat (stream reach) the state of leaf decay is defined by a characteristic fungal assemblage and vice versa. This does not preclude, however, that various stages of decay and succession co-occur on a particular leaf or even a leaf disc. The patterns observed in this and other studies rather reflect a 'mean succession' (Frankland, 1981) or, better, average succession of the fungal community, because successional changes occur on small discrete leaf patches. Accordingly, the shift in community structure in the current study was not accompanied by species extinction, as is generally the case with successions of saprotrophic organisms (Frankland, 1981; Swift, 1983). In view of the physiological versatility of aquatic hyphomycetes (e.g. Suberkropp, 1992), their small size and their mycelial growth form (Frankland, 1981; Swift 1983), the sampling grid was certainly too coarse, the changes in substrate quality too small (see Gessner, 1991), and the overall environmental conditions too stable. The obvious changes in the distribution of conidiophores on the leaf surface suggest, however, that a true replacement of species did indeed occur at the mm^2 scale.

In general accordance with literature accounts, *L. centrosphaera*, *T. elegans* (Bärlocher, 1991; but see Chamier & Dixon, 1982), *F. curvula* and partly *L. aquatica* (Suberkropp & Klug, 1976; Chauvet, Mercé & Jean-Louis, 1986; Chergui & Pattee, 1988; Suberkropp *et al.*, 1988; but see Bärlocher & Kendrick, 1974; and Bärlocher, 1991), were associated with short leaf incubation times in the Touyre and can thus be classified as early colonizers. Likewise, *C. longibrachiata* and *H. stellata* can be confidently referred to as late colonizers (Figs 2, 3; Chauvet *et al.* 1986; Bärlocher, 1991), which is consistent with the slow growth of these species in pure culture (unpublished data).

Seasonal colonization patterns

Stable successional patterns, such as those described here for alder leaves colonized by aquatic hyphomycetes during the period of leaf fall, can be modulated by seasonal influences. Suberkropp (1984), in particular, documented for a hard-water lowland stream (Augusta Creek in Michigan) the replacement of a distinct winter community by an equally well-defined summer assemblage. Similarly, Bärlocher (1991) described differences in the community structure of aquatic hyphomycetes on leaf litter that was incubated either in September or in November in a southern English lowland stream (River Teign, Devon). In a series of laboratory and field experiments, these shifts in species composition were correlated with changes in water temperature (Suberkropp & Klug, 1976; Suberkropp, 1984), leading to the formulation of the temperature-threshold hypothesis, according to which the summer assemblage with typical warm-water species such as *Lunulospora curvula* Ingold and *Triscelophorus monosporus* Ingold (Webster, Moran & Davey, 1976; Chauvet, 1991) appears when water temperature permanently exceeds 16–18°. The bloom develops in mid-summer at temperatures of up to 26°. Once established, the summer assemblage dominates until the temperature falls below 5° in late autumn. Strikingly, the differences observed by Bärlocher (1991) between leaf packs submerged in September and November in the River Teign were mainly due to the dynamics of *L. curvula*, which co-dominated the fungal community in September but was no longer found among the abundant species when temperature had dropped below 5° in November.

In the Touyre, the annual temperature range was much smaller than in Augusta Creek and probably also smaller than in the River Teign. Even during the exceptionally hot summer in 1989, when the current experiments were carried out, water temperature hardly ever exceeded 15° during the measurements made every 2 or 4 wk in the mornings (Fig. 1). Accordingly, none of the five warm-water species common to south-western France (including *L. curvula* and *T. monosporus*; Chauvet, 1991) was recorded in the present investigation. Although the composition of fungal communities depends on many factors, some of which may vary with season, it is tempting to argue that the non-exceeding of the threshold temperature in the Touyre prevented the establishment of a

typical summer assemblage in this stream, resulting in an aquatic hyphomycete community dominated by the winter species all year round.

In spite of the striking lack of species replacement in this summer cool mountain stream, there was a tendency in the Touyre for seasonal changes, exhibiting a cyclic pattern on the principal plane of a correspondence analysis (Fig. 4). Three major reasons are probably responsible for this result. First, during the warmer months leaf litter decomposed more rapidly (Table 4). The mature fungal community hence developed faster in spring and summer and more slowly in winter, and as a consequence different successional stages were recorded in different seasons at equal exposure times (Fig. 5). This explanation is consistent with the dynamics of mycelial biomass and conidial production (Table 4), and probably holds particularly true for the projection of the winter series on the outer left margin of the display (Fig. 4). Second, some species of aquatic hyphomycetes that may be typical of cold water (e.g. *L. centrosphaera, Taeniospora gracilis*; Chauvet, 1992) and the mycoparasite *Crucella subtilis* (Marvanová & Suberkropp, 1990) were especially abundant in autumn and winter, while in spring and summer other species such as *T. marchalianum* with a tendency for warmer temperatures (Suberkropp, 1984; Chauvet, 1991) assumed greater importance. Since correspondence analysis emphasizes 'shape' rather than the size of the data (Greenacre, 1984), *T. marchalianum* was clearly associated with the spring and summer samples (Fig. 4), although it never constituted an important component of the community. Third, the inoculum potential (Frankland, 1981) may have varied somewhat with season in the Touyre, and this could have accounted for the greater importance of *C. aquatica* during the warmer months.

Colonization of fresh and air-dried leaf litter

In accordance with the observations made by Bärlocher (1991), the colonization of fresh leaf litter by aquatic hyphomycetes was delayed in the current study. This phenomenon is apparent from both the analysis of fungal community structure (Fig. 6*a–c*) and quantitative data on mycelial biomass dynamics and conidial production (Table 5), and may be related to inhibitory compounds that would be readily removed from dried leaves by leaching (Bärlocher, 1990). However, with leaf decay progressing further, almost identical communities developed on fresh and dried litter (Fig. 6*d, e*), a finding that is consistent both between the two study years and with the results of Bärlocher's (1991) investigation. The differences between fresh and dried leaves observed by this author in early autumn (September) were mainly due to the lower abundance of the summer species *L. curvula* on fresh leaves, obviously caused by the delay in fungal colonization of these leaves and the concurrent drop in water temperature below 5°. Accordingly, no differences emerged when the experiment was repeated in November (Bärlocher, 1991). The equipment of aquatic hyphomycetes with plentiful hydrolytic enzymes (Chamier, 1985; Suberkropp, 1992) that would make them independent of labile carbon sources and their low substrate specificity (Suberkropp, 1992) may have been the major grounds for the parallel development of aquatic hyphomycete communities on fresh and air-dried leaf litter.

We are grateful to Drs Enrique Descals for taxonomic and André Fabre for statistical advice. Professor John Webster kindly commented on the manuscript. This work was supported by a grant to M. O. Gessner from the Commission of the European Communities.

REFERENCES

Bärlocher, F. (1982). On the ecology of Ingoldian fungi. *BioScience* **32**, 581–586.

Bärlocher, F. (1990). Factors that delay colonization of fresh alder leaves by aquatic hyphomycetes. *Archiv für Hydrobiologie* **119**, 249–255.

Bärlocher, F. (1991). Fungal colonization of fresh and dried leaves in the River Teign (Devon, England). *Nova Hedwigia* **52**, 349–357.

Bärlocher, F. & Kendrick, B. (1974). Dynamics of the fungal populations on leaves in a stream. *Journal of Ecology* **62**, 761–791.

Chamier, A.-C. (1985). Cell-wall-degrading enzymes of aquatic hyphomycetes: a review. *Botanical Journal of the Linnean Society* **91**, 67–81.

Chamier, A.-C. & Dixon, P. A. (1982). Pectinases in leaf degradation by aquatic hyphomycetes. I. The field study. The colonization-pattern of aquatic hyphomycetes on leaf packs in a Surrey stream. *Oecologia* **52**, 109–115.

Chamier, A.-C., Dixon, P. A. & Archer, S. A. (1984). The spatial distribution of fungi on decomposing alder leaves in a freshwater stream. *Oecologia* **64**, 92–103.

Chauvet, E. (1991). Aquatic hyphomycete distribution in South-Western France. *Journal of Biogeography* **18**, 699–706.

Chauvet, E. (1992). Dynamique saisonnière des spores d'hyphomycètes aquatiques de quatre rivières. *Nova Hedwigia* **54**, 379–395.

Chauvet, E., Mercé, J. & Jean-Louis, A. M. (1986). Hyphomycètes aquatiques colonisant les feuilles de *Salix alba* L. *Bulletin de la Société de Mycologie de France* **102**, 347–351.

Chergui, H. & Pattee, E. (1988). The dynamics of hyphomycetes on decaying leaves in the network of the River Rhone (France). *Archiv für Hydrobiologie* **114**, 3–20.

Descals, E. & Chauvet, E. (1992). Diversité des champignons Ingoldiens de quelques rivières du sud-ouest de la France. *Nova Hedwigia* **54**, 83–96.

Frankland, J. C. (1981). Mechanisms in fungal successions. In *The Fungal Community: its Organization and Role in the Ecosystem*, 1st edn (ed. D. T. Wicklow & G. C. Carroll), pp. 403–426, Marcel Dekker: New York.

Gessner, M. O. (1991). Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. *Freshwater Biology* **26**, 387–398.

Gessner, M. O., Bauchrowitz, M. A. & Escautier, M. (1991). Extraction and quantification of ergosterol as a measure of fungal biomass in leaf litter. *Microbial Ecology* **22**, 285–291.

Gessner, M. O. & Schwoerbel, J. (1991). Fungal biomass associated with decaying leaf litter in a stream. *Oecologia* **87**, 602–603.

Gönczöl, J. (1989). Longitudinal distribution patterns of aquatic hyphomycetes in a mountain stream in Hungary. Experiments with leaf packs. *Nova Hedwigia* **48**, 391–404.

Greenacre, M. J. (1984). *Theory and Applications of Correspondence Analysis*. Academic Press: London.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211.

Ingold, C. T. (1942). Aquatic hyphomycetes of decaying alder leaves. *Transactions of the British Mycological Society* **25**, 339–415.

Marvanová, L. & Suberkropp, K. (1990). *Camptobasidium hydrophilum* and its anamorph, *Crucella subtilis*: a new Heterobasidiomycete from streams. *Mycologia* **82**, 208–217.

Newell, S. Y. (1992). Estimating fungal biomass and productivity in decomposing litter. In *The Fungal Community: its Organization and Role in the Ecosystem*, 2nd edn (ed. G. C. Carroll & D. T. Wicklow), pp. 521–561. Marcel Dekker: New York.

Shearer, C. A. & Lane, L. C. (1983). Comparison of three techniques for the study of aquatic hyphomycete communities. *Mycologia* **75**, 498–508.

Shearer, C. A. & Webster, J. (1985 *a*). Aquatic hyphomycete communities in the River Teign. I. Longitudinal distribution patterns. *Transactions of the British Mycological Society* **84**, 489–501.

Shearer, C. A. & Webster, J. (1985 *b*). Aquatic hyphomycete communities in the River Teign. III. Comparison of sampling techniques. *Transactions of the British Mycological Society* **84**, 509–518.

Suberkropp, K. (1984). Effect of temperature on seasonal occurrence of aquatic hyphomycetes. *Transactions of the British Mycological Society* **82**, 53–62.

Suberkropp, K. (1992). Aquatic hyphomycete communities. In *The Fungal Community: its Organization and Role in the Ecosystem*, 2nd edn (ed. G. C. Carroll & D. T. Wicklow). Marcel Dekker: New York.

Suberkropp, K. & Klug, M. J. (1976). Fungi and bacteria associated with leaves during processing in a woodland stream. *Ecology* **57**, 707–719.

Suberkropp, K., Michelis, A., Lorch, H. J. & Ottow, J. C. G. (1988). Effect of sewage treatment plant effluents on the distribution of aquatic hyphomycetes in the River Erms, Schwäbische Alb, F.R.G. *Aquatic Botany* **32**, 141–153.

Swift, M. J. (1983). Microbial succession during the decomposition of organic matter. In *Experimental Microbial Ecology* (ed. R. G. Burns & J. H. Slater), pp. 164–177. Blackwell: Oxford.

Thomas, K., Chilvers, G. A. & Norris, R. H. (1991). Changes in concentration of aquatic hyphomycete spores in Lees Creek, ACT, Australia. *Mycological Research* **95**, 178–183.

Webster, J. R. & Benfield, E. F. (1986). Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* **17**, 567–594.

Webster, J., Moran, S. T. & Davey, R. A. (1976). Growth and sporulation of *Tricladium chaetocladium* and *Lunulospora curvula* in relation to temperature. *Transactions of the British Mycological Society* **67**, 491–495.