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Aquatic hyphomycete distribution in South-Western France

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Abstract. In a survey of aquatic hyphomycetes in South-Western France, the species composition of conidia in foam samples was analysed at twenty-seven stations located on different streams. Correspondence analysis was used to examine the relationships between general distribution patterns of the hyphomycete species and some external factors (altitude, pH, temperature, and season). With respect to the first two axes determined, a group of five species (*Campylospora chaetocladia* Ranzoni, *Campylospora* sp., *Heliscus tentaculus* Umphlett, *Lunulospora curvula* Ingold and *Triscelophorus monosporus* Ingold) emerged and was clearly associated with typical lowland streams with high pH and temperature. In a second analysis, in which these five species and nineteen rare species were excluded, two species (*Clavatospora longibrachiata* (Ingold) Marvanová

and S. Nilsson and *Tetrachaetum elegans* Ingold) appeared characteristic of acid water (pH<6), low altitude and autumn months. Many of the remaining species were essentially discriminated in relation to altitude. *Tetrachidium marchalianum* de Wildeman, *Tricladium angulatum* Ingold and *Tricladium gracile* Ingold were typical of lowland streams, whereas *Taeniospora gracilis* Marvanová and *Tricladium chaetocladium* Ingold were generally found in mountain streams. Compared to the effect of altitude, water pH seemed to be of secondary importance in this region.

Key words. Fungi, aquatic hyphomycete, distribution, stream, South-Western France, correspondence analysis.

Résumé. Un inventaire des espèces d'hyphomycètes aquatiques présentes dans l'écume des cours d'eau a été réalisé dans vingt-sept stations du sud-ouest de la France. L'analyse des correspondances a permis de déterminer les relations entre la distribution des espèces d'hyphomycètes et plusieurs facteurs externes (altitude, pH, température et saison). Un groupe de cinq espèces (*Campylospora chaetocladia* Ranzoni, *Campylospora* sp., *Heliscus tentaculus* Umphlett, *Lunulospora curvula* Ingold et *Triscelophorus monosporus* Ingold) a pu être distingué dans le plan des deux premiers axes de l'analyse et était associé à des rivières de plaine caractérisées par des pH et des températures élevées. Dans une seconde analyse où ces cinq espèces et dix-neuf espèces rares ont été exclues, deux espèces (*Clavatospora longibrachiata* (Ingold) Marvanová

et S. Nilsson et *Tetrachaetum elegans* Ingold) apparaissaient liés à des eaux acides (pH<6), des altitudes faibles et les mois d'automne. Le facteur de discrimination de la plupart des autres espèces était l'altitude. *Tetrachidium marchalianum* de Wildeman, *Tricladium angulatum* Ingold et *Tricladium gracile* Ingold étaient typiques des rivières de basse altitude tandis que *Taeniospora gracilis* Marvanová et *Tricladium chaetocladium* Ingold étaient principalement observés dans les cours d'eau de montagne. Dans cette partie de la France, l'effet du pH est apparu secondaire en comparaison avec l'influence de l'altitude.

Mots clés. Champignon, hyphomycète aquatique, distribution, rivière, sud-ouest de la France, analyse des correspondances.

INTRODUCTION

A number of environmental factors have been demonstrated to affect the distribution of aquatic fungi. Spatial and seasonal occurrence of aquatic hyphomycetes has been shown to be related to both water temperature (Suberkropp, 1984) and pH (Bärlocher, 1987; Chamier, 1987, 1990; Wood-Eggenschwiler & Bärlocher, 1983). The importance

of altitude in fungal community composition has been suggested by longitudinal variations observed along streams (Gönczöl, 1989; Shearer & Webster, 1985a). However, these studies were generally concerned with the effect of only one factor and did not examine other parameters. In the literature on the ecology of aquatic hyphomycetes, few studies have used statistical analyses to compare communities or to examine the effect of environmental factors on

species abundance and distribution. Wood-Eggenschwiler & Bärlocher (1983, 1985) and Shearer & Webster (1985a) compared communities with the Sørensen index. Chauvet & Mercé (1988) used the analysis of variance to differentiate the hyphomycete communities of two regions. As in other fields of ecological research where a large set of data has been collected from many stations, some methods of numerical analysis, such as factor analysis, may highlight the major features of fungi distribution and the influence of environmental parameters (Söderström & Frisvad, 1990).

From twenty-seven stream stations located in the south-west of France, the composition of aquatic hyphomycete community was determined from conidia trapped in foam. Correspondence analysis was used to examine the relationships between the distribution of fungal species and physical parameters (season, altitude, water temperature and pH).

SITES AND METHODS

Twenty-seven stations located on twenty-six streams in South-Western France were investigated (Chauvet, 1989). From the west to the east, the area included stations in the Landes, the Béarn and the Gascogne regions, the Garonne River plain, the Pyrénées mountains and the Montagne Noire (Fig. 1). Most of the streams were located in the Garonne River and Adour River basins (Fig. 2). The altitude of the stations varied between 9 and 935 m, with pH

and temperature values respectively within the ranges 5.0–8.5 and 2–20°C (Table 1). Four stations (H–K) were sampled at 4–5 week intervals for one year whereas the other twenty-three stations were sampled two to four times in autumn, winter and spring. This led to a total of 104 station/time foam samples. Foam was fixed with a solution of formalin, acetic acid and alcohol (Bärlocher, 1987; Ingold, 1975) and conidia were later identified and counted under the microscope. For each sample, ten replicates of 0.1 µl were evaluated. A total of fifty-four hyphomycete species was recorded (Table 1). The frequency of the conidia of each species was represented by a coefficient varying from 0 to 5: 0 = 0%, 1 = 0–1%, 2 = 1–5%, 3 = 5–15%, 4 = 15–60%, 5 = 60–100% of total conidia (Lorillard, 1974).

Correspondence analyses were performed with a micro-computer and the BIOMECA statistics program (Lebreton and coll., C.E.P.E., Montpellier). Graphical displays were obtained with the GRAPHIX program (Lauga, C.E.R.R., Toulouse). Correspondence analyses were used for a total of 104 station/time observations. To describe the effect of external factors on the hyphomycete community, each observation was characterized by five environmental parameters (station, altitude, pH, temperature and month/season). These parameters did not participate in the calculations (determination of the axes) but they have been included in graphical displays in order to assist the interpretation. These supplementary data were coded as a logical indicator

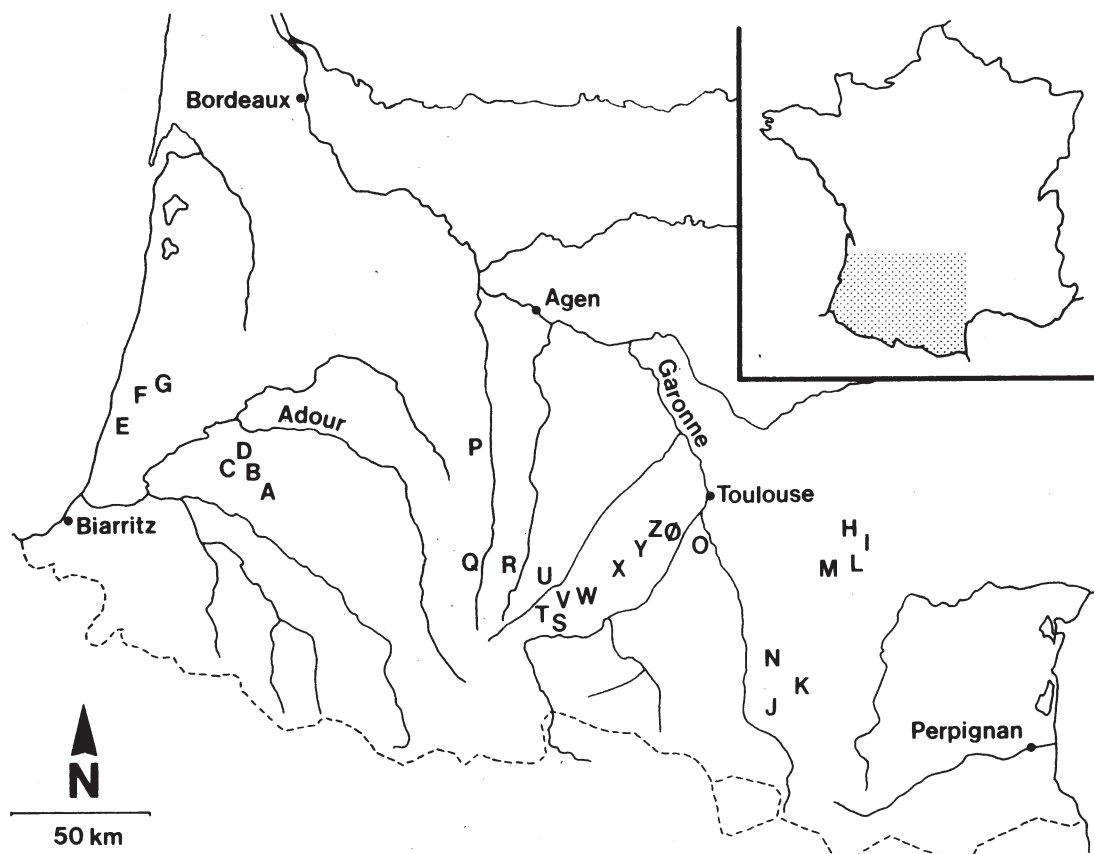


FIG. 1. Location of the twenty-seven stations (A to Ø) in South-Western France.

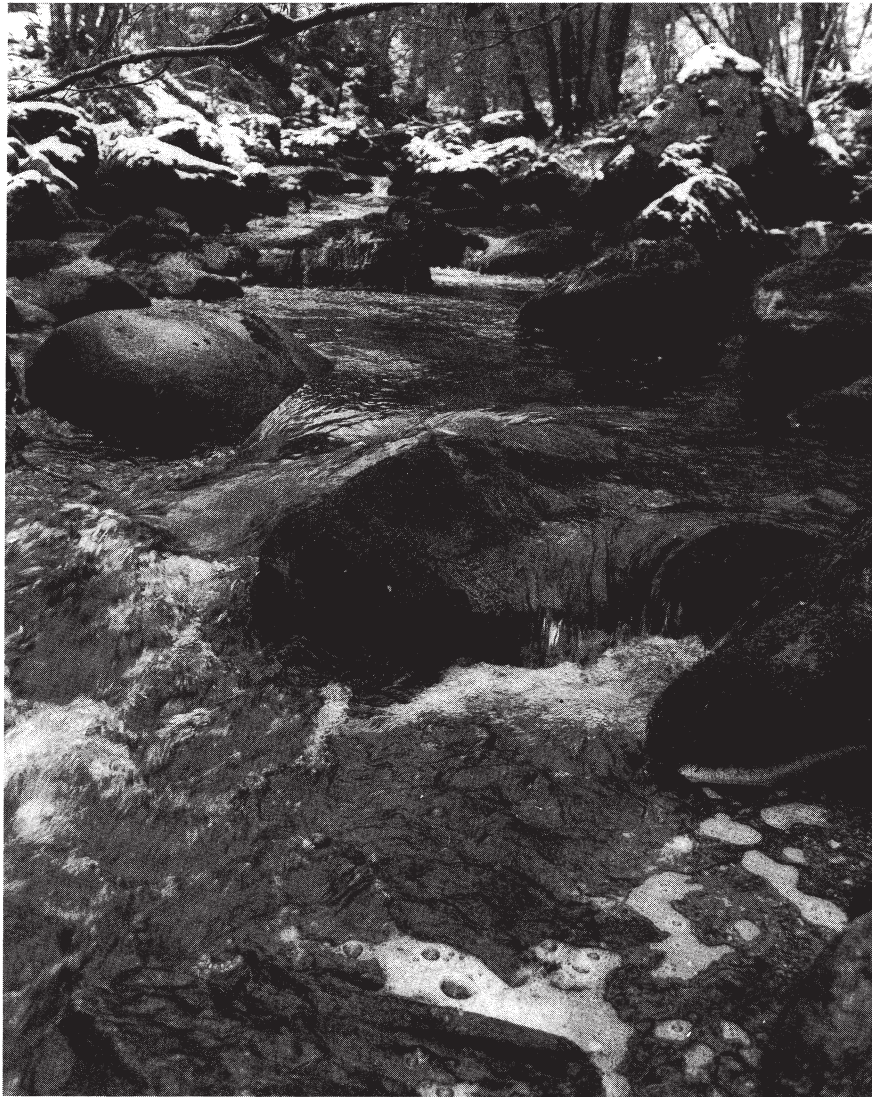


FIG. 2. Sampling station J on the Touyre. Note the freshly formed foam to the bottom right of the picture.

matrix (disjunctive coding). For altitude, temperature and pH, five categories were distinguished. Table 1 indicates the category limits. Time was represented as four seasons and eleven months (September was not represented in the data set). The stations were coded as twenty-seven categories.

RESULTS

The first correspondence analysis was based on the entire data set. In this analysis, the first (F1) and second (F2) principal axes explained 12.8% and 8.6%, respectively, of the total inertia of species distribution. With respect to the F1 and F2 axes, the main group of species was clearly distinct from a group of five species, *Campylospora chaetocladia* Ranzoni, *Campylospora* sp., *Heliscus tentaculus* Umphlett, *Lunulospora curvula* Ingold and *Triscelophorus monospor-*

us Ingold (Fig. 3). External parameters were displayed according to their scores on the same axes (Fig. 3). Three groups of stations could be distinguished and characterized with correspondence to other external parameters. A first group included the stations K, M to P and X which were located in lowland streams with high pH and high temperature. In contrast, a second group (stations H–J and L) was characterized by relatively high altitude, low pH and low temperature. An intermediate group included all the other stations. The space/time arrangement of hyphomycete species may be interpreted according to the display of external factors. The group of five species tended to be associated with low altitude and high temperature ($\geq 16^{\circ}\text{C}$) and pH (≥ 8.0) which were typical of lowland streams (first group of stations). These five species corresponded to the end of summer (August) and the beginning of autumn (October). On the other hand, some species (*Culicidospora aquatica* R.H. Petersen, *Geniculospora inflata* (Ingold) S.

TABLE 1. List of symbols used in the analyses: codes for aquatic hyphomycete species, limits and codes for altitude, temperature and pH categories, codes for seasons and months. The stations are coded as A to Ø symbols.

Species		TO	<i>Triscelophorus monosporus</i> Ingold
AA	<i>Alatospora acuminata</i> Ingold	TP	<i>Tricladium patulum</i> Marvanová and Marvan
AF	<i>Alatospora flagellata</i> (Gönczöl) Marvanová	TR	<i>Volucrispora aurantiaca</i> Haskins
AI	<i>Anguillospora filiformis</i> Greathead	TS	<i>Tetracladium setigerum</i> (Grove) Ingold
AL	<i>Anguillospora longissima</i> (Saccardo and Sydow)	TU	<i>Tumularia aquatica</i> (Ingold) Descals and Marvanová
AM	<i>Actinosporella megalospora</i> (Ingold) Descals and Marvanová	TX	<i>Tetracladium maxilliforme</i> (Rostrup) Ingold
AP	<i>Anguillospora pseudolongissima</i> Ranzoni	TY	<i>Tripospermum myrti</i> (Lind.) Hughes
AR	<i>Anguillospora crassa</i> Ingold	VE	<i>Varicosporium elodeae</i> Kegel
AT	<i>Articulospora tetracladia</i> Ingold	VG	<i>Varicosporium giganteum</i> Crane
AU	<i>Anguillospora curvula</i> Iqbal	VR	<i>Volucrispora graminea</i> Ingold, McDougall and Dann
BT	? <i>Brachiosphaera tropicalis</i> Nawawi		
CA	<i>Clavariopsis aquatica</i> de Wildeman	Altitude (m)	
CC	<i>Campylospora chaetocladia</i> Ranzoni	0	≤A1<50
CG	<i>Culicidospora gravis</i> Petersen	50	≤A2<200
CL	<i>Clavatospora longibrachia</i> (Ingold) Marvanová and S. Nilsson	200	≤A3<400
CP	<i>Campylospora</i> sp. (cf. <i>filicladia</i> Matsushima)	400	≤A4<700
CQ	<i>Culicidospora aquatica</i> R.H. Petersen	700	<A5
CU	<i>Camposporium pellucidum</i> (Grove) Hughes	Temperature (°C)	
DE	<i>Dendrospora erecta</i> Ingold	0	≤T1<4
DS	<i>Diplocradiella scalaroides</i> Arnaud ex M.B. Ellis	4	≤T2<8
FA	<i>Flabellospora acuminata</i> Descals	8	≤T3<12
FC	<i>Flagellospora curvula</i> Ingold	12	≤T4<16
GI	<i>Geniculospora inflata</i> (Ingold) S. Nilsson ex Marvanová and Nilsson	16	≤T5
GM	<i>Goniopila monticola</i> (Dyko) Marvanová and Descals	pH	
GR	<i>Gyoeffya rotula</i> (von Höhnelt) Marvanová	5.0	≤P1<6.0
HL	<i>Heliscus lugdunensis</i> Saccardo and Thérri	6.0	≤P2<6.8
HS	<i>Heliscella stellata</i> (Ingold and Cox) Marvanová and S. Nilsson	6.8	≤P3<7.2
HT	<i>Heliscus tentaculus</i> Umphlett	7.2	≤P4<8.0
LA	<i>Lemonniera aquatica</i> de Wildeman	8.0	≤P5
LC	<i>Lunulospora curvula</i> Ingold	Season	
LE	<i>Lemonniera centrosphaera</i> Marvanová	W	winter
LO	<i>Lemonniera cornuta</i> Ranzoni	SP	spring
LT	<i>Lemonniera terrestris</i> Tubaki	SU	summer
LU	<i>Lateriramusula uni-inflata</i> Matsushima	A	autumn
MA	<i>Mycocentrospora acerina</i> (Hartig) Deighton	Month	
PS	<i>Pyricularia submersa</i> Ingold	J	January
TA	<i>Tripospermum camelopardus</i> Ingold, Dann and McDougall	F	February
TC	<i>Tricladium chaetocladium</i> Ingold	M	March
TD	<i>Tricladium gracile</i> Ingold	AP	April
TE	<i>Tetrachaetum elegans</i> Ingold	MY	May
TG	<i>Taeniospora gracilis</i> Marvanová	JN	June
TI	<i>Triscelophorus</i> sp. (cf. <i>T. sp. 1</i> Ingold 1975)	JL	July
TL	<i>Tricladium splendens</i> Ingold	AU	August
TM	<i>Tetracladium marchalianum</i> de Wildeman	O	October
TN	<i>Tricladium angulatum</i> Ingold	N	November
		D	December

Nilsson ex Marvanová and S. Nilsson and *Tricladium chaetocladium* Ingold) tended to correspond with early spring (April) and mountain stations. In this analysis, the F1 factor appeared principally related to variations in altitude, whereas the separation of the two groups of species was mainly related to temperature and pH gradients. However, the principal axes of this first analysis explained relatively low percentages of the total inertia of species distribution. This was essentially due to the strong influence of the five particular species which biased the calculations for the other species.

To describe the distribution of the main group of species, a second analysis was then performed excluding the five species associated with lowland, hardwater and relatively warm streams (*C. chaetocladia*, *Campylospora* sp., *H. tentaculus*, *L. curvula* and *T. monosporus*) and nineteen rare species (coefficient of abundance ≤1). Thirty species were used in this analysis (Fig. 4). The principal axes, F1 and F2, explained 18.3% and 10.8%, respectively, of the total inertia of species distribution. A large group of species was distributed along the F1 axis and two species (*Clavatospora longibrachia* (Ingold) Marvanová and S. Nilsson and *Tet-*

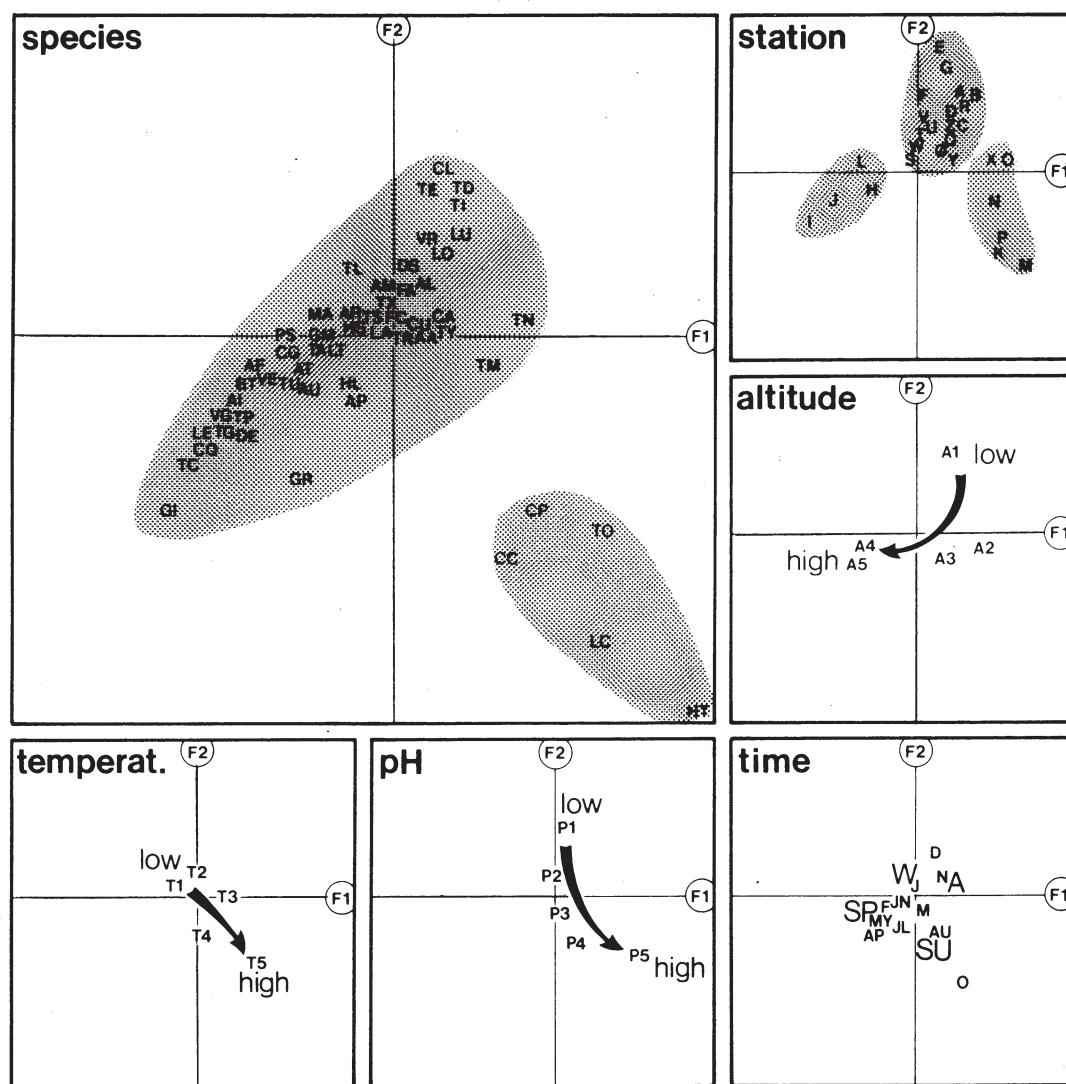


FIG. 3. Display of the fungal species, the stations and the altitude, temperature, pH and time (season and month) categories with respect to the F1 and F2 axes of the first correspondence analysis. The display for the parameters is drawn at one half the scale for the species (so their relative positions on the display are the same). For symbols, see Table 1.

rachetum elegans Ingold) could be distinguished according to the F2 axis. Altitude appeared to be the factor that varied along the first axis, even more so than in the first analysis. This suggested a strong discrimination of most species in relation to altitude. The second axis F2 was clearly related to pH variations. The display of seasons/months showed a maximal distinction between autumn (November, December) and spring (April, May). Except for station F which was characterized by both very low altitude and pH, the stations were mainly distributed along the F1 axis (but some stations in which the excluded species were found could not be represented within the display limits). Therefore the two species (*C. longibrachiata* and *T. elegans*) appeared characteristic of very low altitude (<50 m) and acid water (pH<6.0) and tended to occur in autumn.

In both analyses, the display of F3 and F4 axes did not give more interpretable information.

DISCUSSION

Foam sampling has been widely used in studies of hyphomycete distribution. One of the main problems with this technique is that it is subject to several areas of bias, but in the present study these are considered to have been overcome sufficiently not to affect the result of the survey. (1) The abundance of spores in foam is related not only to the sporulation of hyphomycetes, but also to the quality of foam which varies in time and space. However, relative abundance of species (which was used in this study) is not affected by this parameter. (2) The efficiency of foam in trapping hyphomycete spores varies with species, with specific spore shapes being particularly under-represented (Iqbal & Webster, 1973; Chauvet, unpublished data). For any given species, however, trapping efficiency can be assumed to be relatively constant in foam from different streams. Therefore, it is possible to consider the occurrence

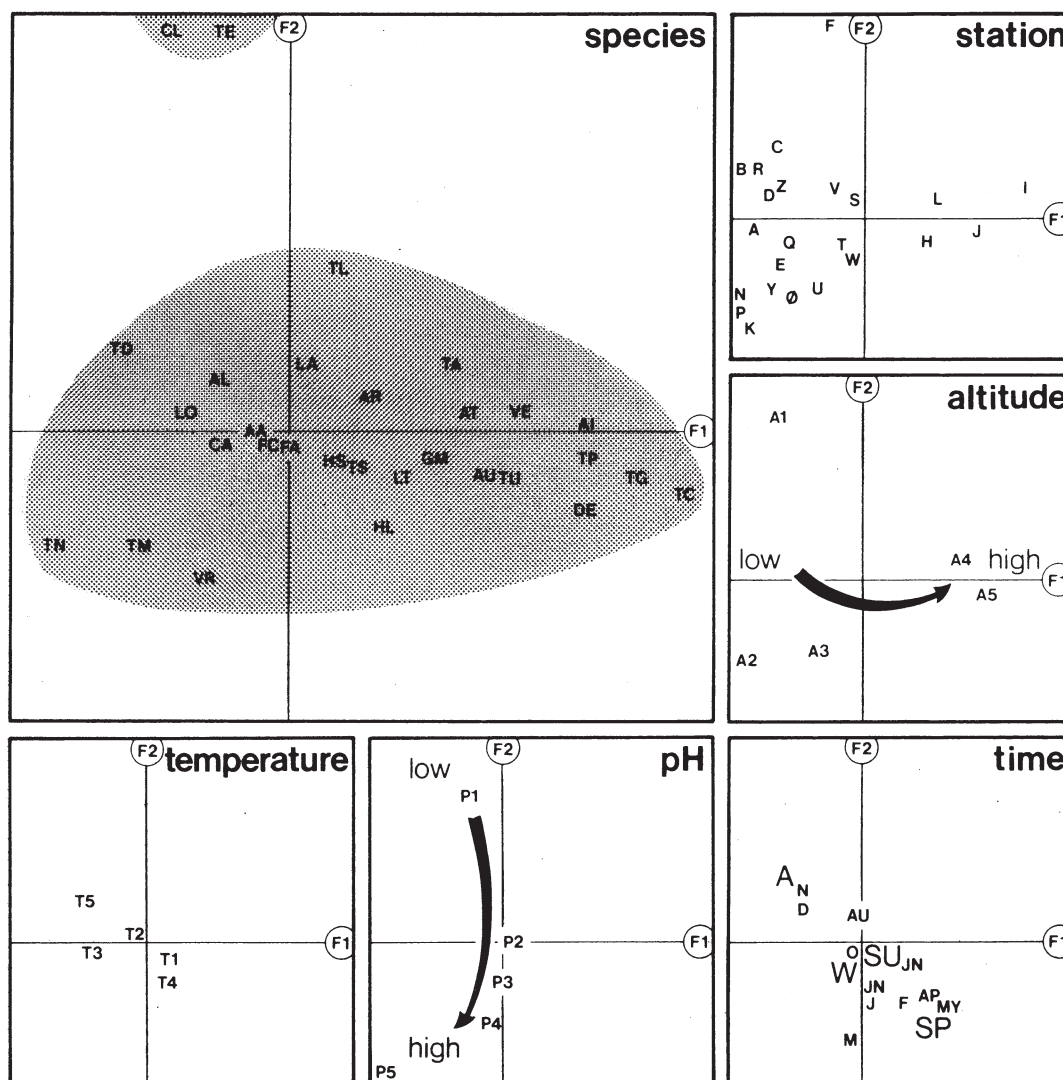


FIG. 4. Display of the fungal species, the stations and the altitude, temperature, pH and time (season and month) categories with respect to the F1 and F2 axes of the second correspondence analysis. Species CC, CP, HT, LC, TO and nineteen rare species were excluded. Stations G, M, O and X were strongly influenced by excluded species and could not be displayed. The display for the parameters is drawn at one half the scale for the species (so their relative positions on the display are the same). For symbols, see Table 1.

of each species in relation with time/space parameters. (3) Since foam traps spores coming from upstream, the species composition of foam is related to a portion of stream whose length is usually unknown. Recently, Thomas, Chilvers & Norris (1990) have shown that the distance hyphomycete spores were carried depended on the species, but that several species were characterized by a persistence of 0.7–0.8 km, expressed as half-life in the stream. Within such short distances, the characteristics of the station (altitude, pH, temperature) can be assumed to vary very little, and species composition will be fairly representative of the station where foam is collected. (4) Foam is likely to persist at the surface of the stream for several days, possibly a few weeks, but probably less than 1 or 2 months. To minimize this effect, fresh foam was sampled in fast-running zones, where it will be constantly replaced (Fig. 2). The possible bias in time was assumed to be less than about 1 month and

not to interfere with seasonal patterns.

The correspondence analyses have emphasized some affinities of species for particular biotopes. In our region, *Campylospora chaetoclada*, *Campylospora* sp., *Heliscus tentaculus*, *Lunulospora curvula* and *Triscelophorus monosporus* were found in lowland streams with hard and relatively warm water. Moreover these species were principally noted in summer and in the beginning of autumn. These observations were in accordance to previous studies (Suberkropp, 1984) and to their main distribution areas which are tropical or subtropical. Wood-Eggenschwiler & Bärlocher (1985) noticed that temperate regions of the Northern Hemisphere could accommodate both cold-adapted species in winter and warm-adapted species (such as *C. chaetoclada* and *L. curvula*) in summer.

Within the studied area, *Clavatospora longibrachiata* and *Tetrachaetum elegans* occurred in acid water which is

typical of some regions, such as the Landes. According to the second analysis, both species were associated with the autumn months and very low altitude. However, the interpretation of the last factor was biased because these very low altitudes, in our data set, were only found in the Landes and Béarn stations (B–G) which also typically had low pH.

The factor which appeared to allow discrimination among most species was altitude, as shown in the second analysis. Some species, such as *Tricladium chaetocladium* and *Taeniospora gracilis* Marvanová, were typically related to mountain streams. Others, such as *Tetracladium marchalianum* de Wildeman, *Tricladium angulatum* Ingold and *Tricladium gracile* Ingold, were characteristic of lowland rivers. However, the latter group seemed to be less favoured by elevated temperature than the first species association (*C. chaetocladia*, *Campylospora* sp., *H. tentaculus*, *L. curvula* and *T. monosporus*). Between these two extremes there was a continuum of species which exhibited some affinity with intermediate altitude. There was also a group of very common species, such as *Alatospora acuminata* Ingold, *Flagellospora curvula* Ingold and *Lemonniera aquatica* de Wildeman whose abundance was not affected by altitude. Displays of these species were always close to the F1 origin (they generally had very low coordinates with all axes). This could be interpreted as the characteristic of widespread species, occurring in a great variety of biotopes.

Compared to the influence of altitude, the importance of pH in our study was lower, since in both correspondence analyses the latter factor only corresponded to the second axis F2. However, our results suggested that pH may affect the distribution of some species, such as *C. chaetocladia*, *Campylospora* sp., *H. tentaculus*, *L. curvula*, *T. monosporus* (high pH) and *C. longibrachiata* and *T. elegans* (low pH). Most other species appeared to occur in our streams with pH within the range 6.0–8.0. These values are typical of most natural waters in South-Western France. Values of pH close to neutrality have been previously reported to coincide with maximum species richness in aquatic hyphomycete (Shearer & Webster, 1985a; Marvanová, 1984; Wood-Eggenschwiler & Bärlocher, 1983; Bärlocher & Rosset, 1981). However, the number of aquatic hyphomycete species in Canadian woodland streams was recently found to be stable or to decline slightly with pH from 5 to 7 (Bärlocher, 1987). This author suggested that factors other than acidity (e.g. the lack in riparian trees) explained the low species richness observed in moorland streams (Shearer & Webster, 1985a; Iqbal & Webster, 1977). A comparable phenomenon may occur in our most acid streams. These streams which were mainly found in the Landes region were almost exclusively bordered by pine trees (Chauvet & Mercé, 1988) and had low numbers of fungal species. Although aquatic hyphomycete may colonize conifer needles (Bärlocher & Oertli, 1978; Bärlocher, Kendrick & Michaelides, 1978) the number of species on conifer litter has been shown to be much lower than on deciduous leaves (Bärlocher, 1982).

Seasonal changes in aquatic hyphomycete communities have been previously documented (Shearer & Webster, 1985b; Suberkropp, 1984; Iqbal, Bhatti & Malik, 1979; Gönczöl, 1975; Triska, 1970). These variations have been

generally attributed to the effect of temperature (Suberkropp, 1984). The composition of leaf substrata has been also mentioned (Webster & Descals, 1981). Our results showed a greater effect of time than of temperature for most species. This suggests the influence of other time related factor(s), such as the water chemistry or the quantity and quality of available substrata.

Temperature, associated with pH, appeared to be a factor of discrimination of some hyphomycete species (first analysis). However, the role of temperature for most species (second analysis) seemed to be not clearly determinant since different categories of temperature were closely represented in the display, whatever the considered axis. In our region, temperature controls the occurrence of few warm-dependent species, such as *C. chaetocladia*, *H. tentaculus*, *L. curvula* and *T. monosporus*. This group of species was generally associated with temperature above 16–18°C. Below this value, the other species seemed to be not influenced by temperature. This is consistent with previous results on the influence of temperature on aquatic hyphomycete (Suberkropp, 1984). As the temperature of Michigan streams approached or exceeded about 20°C, a summer assemblage of few species including *Flagellospora penicilloides* Ingold, *H. tentaculus*, *L. curvula* and *T. monosporus* dominated a winter assemblage of species. Once established on leaves, either assemblages could maintain dominance, depending on whether the temperature was increasing or decreasing. Thus the effect of temperature followed a bimodal pattern with a clear separation of species in two groups. Our first analysis emphasized this distinction. No gradual effect of temperature was found amongst cold-season species which formed the bulk of the hyphomycete communities in South-Western France. Thus the importance of altitude on hyphomycete distribution suggested by our data (second analysis) appeared to be the expression of factors other than temperature. Inter-specific competition could be superposed on the temperature factor. Then it could mask or alter the effect of temperature as shown in experiments with *L. curvula* and *T. chaetocladium* (Webster, Moran & Davey, 1976). In this interaction process, the nature of substrata could play a greater role than generally assumed. However, the importance of substrata has been recently emphasized in the studies of Chamier (1987) and Shearer & Zare-Maivan (1988). To some extent the distribution of tree species, i.e. plant matter quality, may be expressed as a function of altitudinal gradient. For instance, hardwood tree species are principally found in the upper part of drainage basins whereas softwood species are more characteristic of the lower part. Moreover the timing of leaf litter input varies with altitude. Further studies on aquatic hyphomycete distribution should include information on availability and quality of substrata in the ecosystem.

In conclusion, four distinct associations emerged from the factor analysis:

(1) *Campylospora chaetocladia*, *Campylospora* sp., *Heliscus tentaculus*, *Lunulospora curvula* and *Triscelophorus monosporus* occurred in lowland streams characterized by high pH and relatively high water temperature. Abundance maxima were found in summer and in early autumn.

(2) Likewise, *Tetracladium marchalianum*, *Tricladium angulatum* and *T. gracile* were typical of lowland streams. However, compared to the first association, this group seemed to be less favoured by elevated temperature.

(3) *Tetrachaetum elegans* and *Clavatospora longibrachiatata* tended to occur in acidic streams at the end of summer and in early fall.

(4) *Tricladium chaetocladium* and *Taeniospora gracilis* were generally found in mountain streams.

There was also a group of common species such as *Alatospora acuminata*, *Flagellospora curvula* and *Lemonniera aquatica* whose abundance was not associated to any of the parameters considered.

On the whole, the influence of both altitude and season did not appear to be directly related to temperature. A possible explanation is that the species assemblage is determined by substrata quality varying with riparian vegetation and timing of litter input along altitudinal gradients.

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