

## Aquatic hyphomycetes in Catamaran Brook: colonization dynamics, seasonal patterns, and logging effects

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**Abstract:** Aquatic fungal colonization dynamics and seasonal patterns were investigated in two sites in Catamaran Brook, New Brunswick, Canada, as part of a larger study to evaluate logging effects on a salmon stream. Four leaf-pack trials were conducted between May 1995 and Dec 1996 to determine species composition of the fungal community, the seasonal pattern of colonization on decaying maple leaves, and what effects, if any, invertebrate feeding and logging activities might have on community structure. Contrary to expectation, neither mesh size (i.e., invertebrate presence or absence) nor preliminary logging activity (road construction near one site) had a consistent effect on community structure. Time of immersion of the leaves in the stream, followed by season, were the major factors controlling community structure. Spore production and species diversity measures were highest during the middle part of the colonization period (generally 4–8 wk of immersion in summer trials and 2–4 wk immersion in the autumn trial), and were also higher in the autumn (Sep to Dec) than in the summer trials. Forty-five species of hyphomycetes were recorded during the study period, although 6 taxa (*Alatospora acuminata*, *Anguilospora filiformis*, *Articulospora tetracladia*, *Geniculosporea inflata*, *Lunulospora cymbiformis*, and a sigmoid species, probably *Flagellospora curvula*) made up nearly 95% of all identified spores. A total of 35 species were found during the autumn trial, compared to 27 in each of the two summer trials, and 25 during a winter trial. Colonization dynamics also varied with season, but generally there were three main colonization patterns; some taxa were only present or showed highest abundance very early in the colonization period, most arrived or peaked during inter-

mediate stages of leaf decay, and a few were characteristic of the latest stages.

**Key Words:** aquatic fungi, leaf decomposition, New Brunswick, sedimentation

### INTRODUCTION

The decomposition of fallen leaves and other detritus in streams is dominated by fungi (Bärlocher 1992a). Some terrestrial species may begin colonization before leaf abscission and initiate breakdown if conditions are suitable (Bärlocher and Kendrick 1974, Kaushik and Hynes 1971). In streams, however, they are rapidly displaced by aquatic hyphomycetes, a group of fungi with obvious morphological and enzymatic adaptations to life in running water (Rodrigues and Graça 1997, Suberkropp 1992).

Species assemblages of aquatic hyphomycetes vary seasonally, from leaf to leaf and from site to site, depending on a variety of factors (Bärlocher 1992a). Seasonal and latitudinal changes are thought to be mainly due to differences in water temperature (Bärlocher and Kendrick 1974, Iqbal and Webster 1973, Suberkropp 1984, 1992), which can result in distinct summer and winter assemblages in temperate streams (Suberkropp 1984). Site differences within a stream are most closely correlated with altitude or factors associated with it (Fabre 1998, Raviraja et al 1998a), which may include shifts in water chemistry, current or riparian vegetation (Gönczöl 1989, Raviraja et al 1998b, Shearer and Webster 1985). Variability among individual leaves collected from the same site is great, and close intermingling of many different species indicates that strongly antagonistic interactions are rare (Shearer and Lane 1983). Generally, leaves have to be immersed in a stream for 7–12 d before detectable numbers of conidia of aquatic hyphomycetes are produced. Species diversity generally reaches a maximum within 4–6 wk, and subsequently remains stable or gradually declines.

Fungal colonization of wood blocks (Sanders and Anderson 1979) or leaves (Bärlocher and Schweizer 1983) is correlated with surface area of the substrate. Initial fragmentation by the current or by leaf-shredding invertebrates opens new areas for colonization and may result in rapidly increasing fungal diversity. Ultimately, however, leaf breakdown will reduce the

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amount of available substrate and fungal diversity and abundance will decline. Not surprisingly, reduced leaf-shredding activity has been connected with increased fungal spore production (Bärlocher 1980, Suberkropp and Wallace 1992). Its effect on fungal species richness is less clear.

Chamier et al (1984) emphasized the ecological significance of the structure of the fungal community. For example, some fungal species make leaves more palatable and nutritious to invertebrate shredders than others (Rong et al 1995). Anthropogenic activities with the potential of disrupting fungal communities may therefore have implications for the entire food web. In order to understand such disturbances, it is important to compare the seasonal patterns in fungal community structure with or without disturbance.

Catamaran Brook (New Brunswick) is a small salmon stream that has been the site of a multidisciplinary study into the effects of timber harvest since 1990 (Cunjak 1995). The study design included a 5-yr pre-harvest phase to provide baseline data for subsequent comparisons with a 5-yr harvest phase, followed by a 5-yr recovery phase. In this study, we investigated the fungal species assemblage in summer and fall of 1995 (final year of preharvest phase) and winter and summer 1996 (following initiation of logging activity) at two sites, one in the harvest zone, the other outside the harvest zone. Our first goal was to establish fungal colonization patterns during the prelogging phase as influenced by season and site, and the presence/absence of macroinvertebrates. The next step was to discover to what extent these patterns changed with the onset of logging.

#### MATERIALS AND METHODS

**Site descriptions.**—Catamaran Brook ( $46^{\circ} 52.7' N$ ,  $66^{\circ} 6.0' W$ ) is a tributary of the Little Southwest Miramichi River located in north central New Brunswick (FIG. 1). During the preharvest phase of the study (1990–1994), data were collected on physicochemical aspects of the stream (Cunjak et al 1993) and on biological interactions at all trophic levels (Cunjak 1995). Road construction in the basin began during late autumn of 1995, and logging began late in 1996. Road construction activities resulted in increased turbidity in Nov 1995 in one study site (the Gorge Reach site, see below), but no other logging related impacts were noted during the study period. Timber harvest, which was initiated later than expected in the watershed following the termination of this study, subsequently resulted in severe sedimentation to the Gorge Reach (Daniel Caissie, Department of Fisheries and Oceans, Moncton, New Brunswick, pers comm).

Catamaran Brook is a third order stream, 20.5 km in length, with a drainage area of 52 km<sup>2</sup> (Cunjak et al 1990).

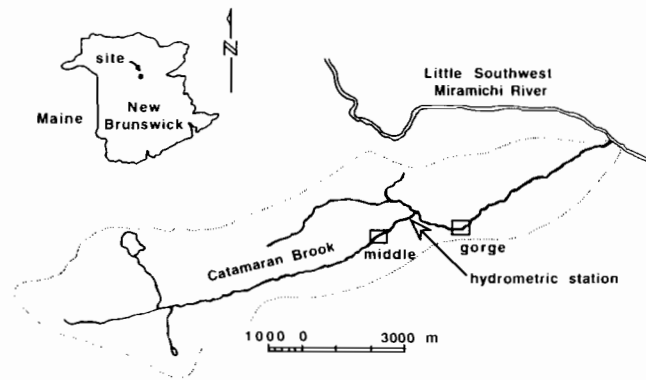


FIG. 1. Catamaran Brook, New Brunswick, showing location of sampling sites and gauging station. Logging cut blocks were located in the headwater zone and adjacent to the Gorge site.

Riparian vegetation in the basin consists of 60% deciduous trees, including white birch (*Betula papyfera*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American Beech (*Fagus grandifolia*), trembling aspen (*Populus tremuloides*), and speckled alder (*Alnus rugosa*). The remaining 40% of forest cover consists of conifers, including balsam fir (*Abies balsamea*), spruce (*Picea* spp.), hemlock (*Tsuga* sp.), and cedar (*Thuja* sp.) (Cunjak et al 1990). Logging activities have been restricted to the upper and middle portions of the basin, and sites for this study were chosen to provide a low-impact site (Middle Reach, far distant from logging activity) and an impact site (Gorge Reach, located in a logging zone) (FIG. 1).

The two sites were chosen to be as similar to each other as possible; both are shallow (approx 0.10 m deep during summer) riffle sites, bordered by alder on the stream banks with mixed forest farther away from the stream. At both sites, the underlying substrate consists primarily of gravel and cobble. The Gorge (impact) site, however, is wider than the Middle (low-impact) site, and therefore receives more light.

Discharge and temperature were monitored continuously at a permanent gauging station (jointly maintained by Environment Canada and Fisheries and Oceans Canada) located about halfway between the two sampling sites (FIG. 1), and water chemistry was analyzed from monthly water samples collected near the gauging station.

**Trials.**—Four trials were conducted: two 12-wk trials during summer, one 12-wk trial during the fall, and one 23-wk trial during the winter, under the ice. The summer 1995 trial was conducted from May 24 to Aug 15, 1995; fall 1995 from Sep 22 to Dec 14, 1995; winter 95/96 from Dec 14, 1995, to May 22, 1996, and summer 1996 from May 22 to Aug 14, 1996. One of the trials (fall 1995) coincided with some pre-logging activity (primarily road building); a second (winter 95/96) took place immediately afterwards. The only noticeable effect on stream physics and chemistry was increased turbidity during Nov 1995 (see FIG. 2).

For each trial, maple leaves (~70% *Acer saccharum* and 30% *Acer rubrum*) were collected from the stream banks,

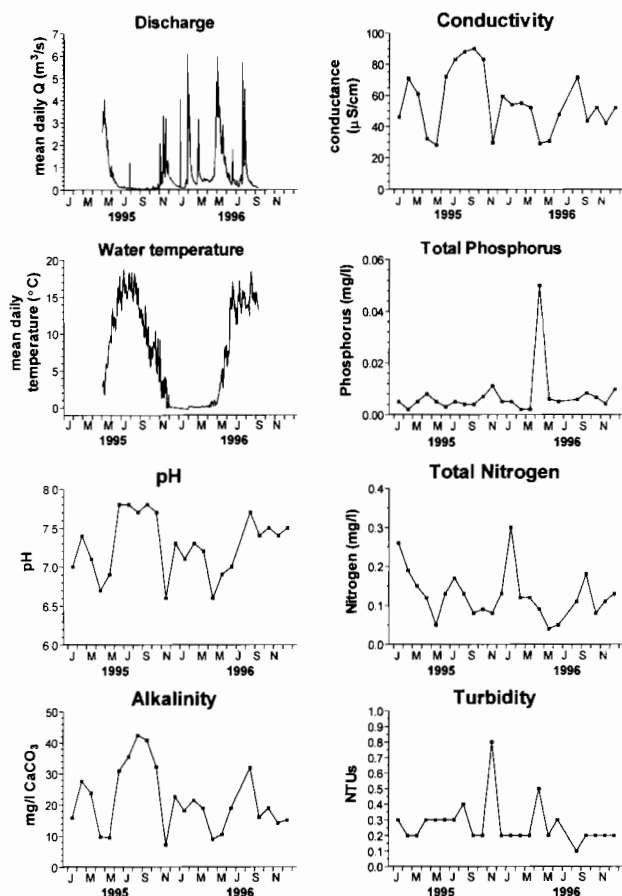


FIG. 2. Physicochemical data for Catamaran Brook, 1995–1996.

cleaned of sediment and airdried. Dried leaves were divided into  $5 \pm 0.05$  g aliquots for the summer 1995 trial and  $3 \pm 0.05$  g aliquots for subsequent trials (5 g aliquots resulted in too concentrated a leaf pack, so the amount was reduced to 3 g in subsequent trials), then placed into  $12 \times 12$  cm fine or coarse-mesh bags and immersed in the brook. Fine-mesh bags were constructed of  $200 \mu\text{m}$  Nitex® to exclude macroinvertebrates. Coarse-mesh bags were constructed of 13 mm Vexar® to allow entry by macroinvertebrates. One each of a fine-mesh bag and a coarse-mesh bag were attached to 25 chimney bricks and placed into a  $5 \times 5$  grid in each site for all trials except the winter 1995/96 trial (due to inaccessibility of the site during winter, only five bricks were used for this trial, and all were collected after 23 wk of immersion). Individual bricks were placed 0.5 m apart in a grid pattern. Five bricks were collected at random from each site after 1, 2, 4, 8, and 12 wk of immersion (except the winter trial), resulting in five fine-mesh and five-coarse mesh bags from each site on each date. Leaves were rinsed with distilled water to remove sediment and invertebrates, which were retained for additional study. Five leaves from each leaf pack were aerated for 48 h at 18 C in a 500-mL Erlenmeyer flask containing 300 mL of distilled, sterilized water to induce spore formation and detachment. After shaking the flasks to free attached spores, water sam-

ples were filtered through  $8 \mu\text{m}$  membrane filters and stained with cotton blue in lactophenol. Filters were cleared by incubating in lactic acid for 45 min at 37 C, then mounted on microscope slides with a further drop of lactic acid. Spores were identified and enumerated by examining the filters with a compound microscope; identifications were based on keys by Nilsson (1964), Ingold (1975), and Marvanová and Descals (1985). Generally, 200–300 spores per filter were identified to determine percentage distribution among the dominant species. In addition, the entire slide was scanned to pick up the less common species. The leaves from the individual flasks were collected, dried at 70 C for 48 h and weighed. This allowed us to calculate spore production per mg dry leaf mass.

The effects of site, mesh size and time on the fungal community were examined by cluster analysis and principal component analysis (SYSTAT 5.2.1 for Macintosh; Erman and Erman 1995, Manly 1986). In addition, we determined fungal species richness (overall number of species, plus number of species per leaf), Shannon diversity (H) and Hurlbert evenness (v), and analyzed for effects of mesh size (fine vs coarse), time of immersion (wk) and site (Middle vs Gorge) on spore production and species diversity measures with a fully factorial ANOVA (for a discussion of some of these measures, see Smith and Wilson 1996).

## RESULTS

Water temperature was constant near 0 C from Dec 1 through Mar 1, and ranged from 10 to 25 C during the summer months, resulting in a maximum mean daily temperature of 19 C in Jul (FIG. 2). Stream discharge ranged from a summer low of  $0.038 \text{ m}^3/\text{s}$  in 1995 to a maximum of  $6.1 \text{ m}^3/\text{s}$  during a winter event in Mar 1996. Discharge was generally low during the summer of 1995 with only one small flood event in Jul. In contrast, there were a number of major floods during the autumn of 1995 and the summer of 1996 (FIG. 2). Catamaran Brook is a circumneutral stream (average pH = 7.26) with generally low alkalinity, conductance and nutrient levels (FIG. 2).

*Taxonomy and community patterns.*—A total of 45 species of fungi (TABLE I) were identified for all sample periods in Catamaran Brook, including two previously undescribed species (unknown 1 and unknown 2). In addition, some sigmoid spores could not be separated and identified with certainty. They were divided into two groups based on size. Most of the smaller spores ( $50\text{--}150 \mu\text{m}$ ) probably belonged to *Flagellospora curvula* (L. Marvanová, Czech Culture Collection, pers comm).

The six most abundant taxa accounted for nearly 95% of all identified spores (TABLE I), and were found in virtually all samples on most dates (FIGS. 3–5). A total of 35 species were found in the fall trial, compared to 27 in each summer trial, and 25 on

TABLE I. Fungal species associated with maple leaves in litterbag trials in Catamaran Brook, N.B., summer 1995 to fall 1996

Fungal species	No./g dry leaf <sup>a</sup>	% of total <sup>a</sup>
<i>Alatospora pulchella</i>	31.0	0.01
<i>Alatospora acuminata</i>	20 052.0	8.02
<i>Anguillospora filiformis</i>	49 241.0	19.69
<i>Anguillospora longissima</i>	1276.0	0.51
<i>Articulospora antipodea</i>	338.0	0.14
<i>Articulospora atra</i>	2527.0	1.01
<i>Articulospora tetracladia</i>	30 346.0	12.14
<i>Articulospora</i> sp.	0.2	0.00
<i>Candida aquatica</i>	25.2	0.01
<i>Clavariopsis aquatica</i>	739.0	0.30
<i>Clavatospora longibrachiata</i>	702.0	0.28
<i>Culicidospora aquatica</i>	269.0	0.11
<i>Culicidospora gravida</i>	0.2	0.00
<i>Dendrospora fusca</i>	10.0	0.00
<i>Dendrospora</i> sp.	6.0	0.00
<i>Diplocyadiella</i> sp.	0.5	0.00
<i>Filosporella</i> sp.	186.0	0.07
<i>Fusarium</i> sp.	994.0	0.40
<i>Geniculospora inflata</i>	29 655.0	11.86
<i>Heliscus lugdunensis</i>	3104.0	1.24
<i>Lambdasporium viridense</i>	1001.0	0.40
<i>Lemonnieria aquatica</i>	2059.0	0.82
<i>Lemonnieria centrosphaera</i>	1055.0	0.42
<i>Lemonnieria terrestris</i>	1362.0	0.54
<i>Lunulospora cymbiformis</i>	28 340.0	11.34
<i>Mycocentrospora acerina</i>	8.0	0.00
Sigmoid >150 µm	6.0	0.00
Sigmoid <150 µm	75 852.0	30.34
<i>Tetrachaetum elegans</i>	367.0	0.15
<i>Tetracladium marchalianum</i>	68.0	0.03
<i>Tricladium angulatum</i>	100.0	0.04
<i>Tricladium anomalum</i>	0.6	0.00
<i>Tricladium chaetocladium</i>	131.0	0.05
<i>Tricladium eccentricum</i>	0.3	0.00
<i>Tricladium patulum</i>	2.0	0.00
<i>Tricladium terrestre</i>	0.2	0.00
<i>Tripospermum camelopardus</i>	0.5	0.00
<i>Tripospermum myrtii</i>	27.0	0.01
<i>Triscelophorus acuminatus</i>	2.0	0.00
<i>Triscelophorus magnificus</i>	3.0	0.00
<i>Triscelophorus monosporus</i>	55.0	0.02
<i>Triscelophorus</i> sp.	3.0	0.00
<i>Varicosporium elodeae</i>	16.0	0.01
Unknown 1	59.0	0.02
Unknown 2	0.1	0.00

<sup>a</sup> Averages of all field trials.

week 23 of the winter trial. Sixteen species were found in all seasons and trials, and these were generally the ones showing the highest spore abundance (following aeration and filtering). Some relatively rare taxa were only found in one of the trials.

Within each trial, community patterns were investigated with cluster analysis (Pearson's distance, single or average linkage, SYSTAT 5.2.1). Each combination of mesh size (fine or coarse), site (Gorge or Middle) and length of immersion (1, 2, 4, 8, 12 wk) gave one datum. Length of immersion was identified as the single most important variable affecting community structure (FIG. 6). In the summer trials, samples collected after week 1 consistently clustered away from all other samples, and weeks 2–4 and 8–12 tended to cluster together. During the fall trial, the major division appeared between samples of week 1 to 4, and 8 to 12, respectively (FIG. 6). In the last fall sample (12 wk), mesh size may have played a minor role in structuring the community. Principal component analysis revealed essentially the same trends (for detailed results, see Garnett 1998). Overall species similarity among the communities was also most strongly influenced by time of immersion; early samples generally had a similarity of <50 % (Sørensen's index), which gradually increased to a value of approx 85% by week 8 (for complete data, see Garnett 1998). None of these analyses gave any indication that site (and therefore vicinity to logging activity) had a consistent, measurable influence on community structure during summer or fall trials. The effect of length of immersion could not be evaluated for the winter 1995–1996 trial, due to difficulties in retrieving leaf packs under the ice. After 23 wk of decomposition under ice, the main influence on community patterns appeared to be Site. However, distances between the individual clusters were very small (FIG. 6).

Length of immersion (wk) was the only factor consistently to affect reproductive activity (spore production, FIGS. 3–5) and species diversity measures (ANOVA,  $P < 0.05$ ; FIG. 7, TABLE II). Mesh size affected spore production (generally higher spore production in coarse mesh than fine mesh) and some diversity measures in the summer 1995 trial, but these patterns were not consistent among trials.

Species diversity (including Shannon diversity, Richness, and Hurlburt evenness; from FIG. 6) generally increased in early samples, peaked and subsequently declined. The specific patterns varied with season; during the summer trials (May–Aug), richness increased gradually from about 5–10 species per leaf on week 1 to 12–17 species by week 8, declining to 11–15 species by week 12. In contrast, the earliest sample in fall (1 wk) already had >10 species per leaf, and the maximum of 15–17 species per leaf was reached between weeks 2 and 4.

In the first trial potentially influenced by logging (fall 95), site significantly affected fungal species richness and evenness (TABLE II, none had been affected in the prelogging summer trial of 1995). However,

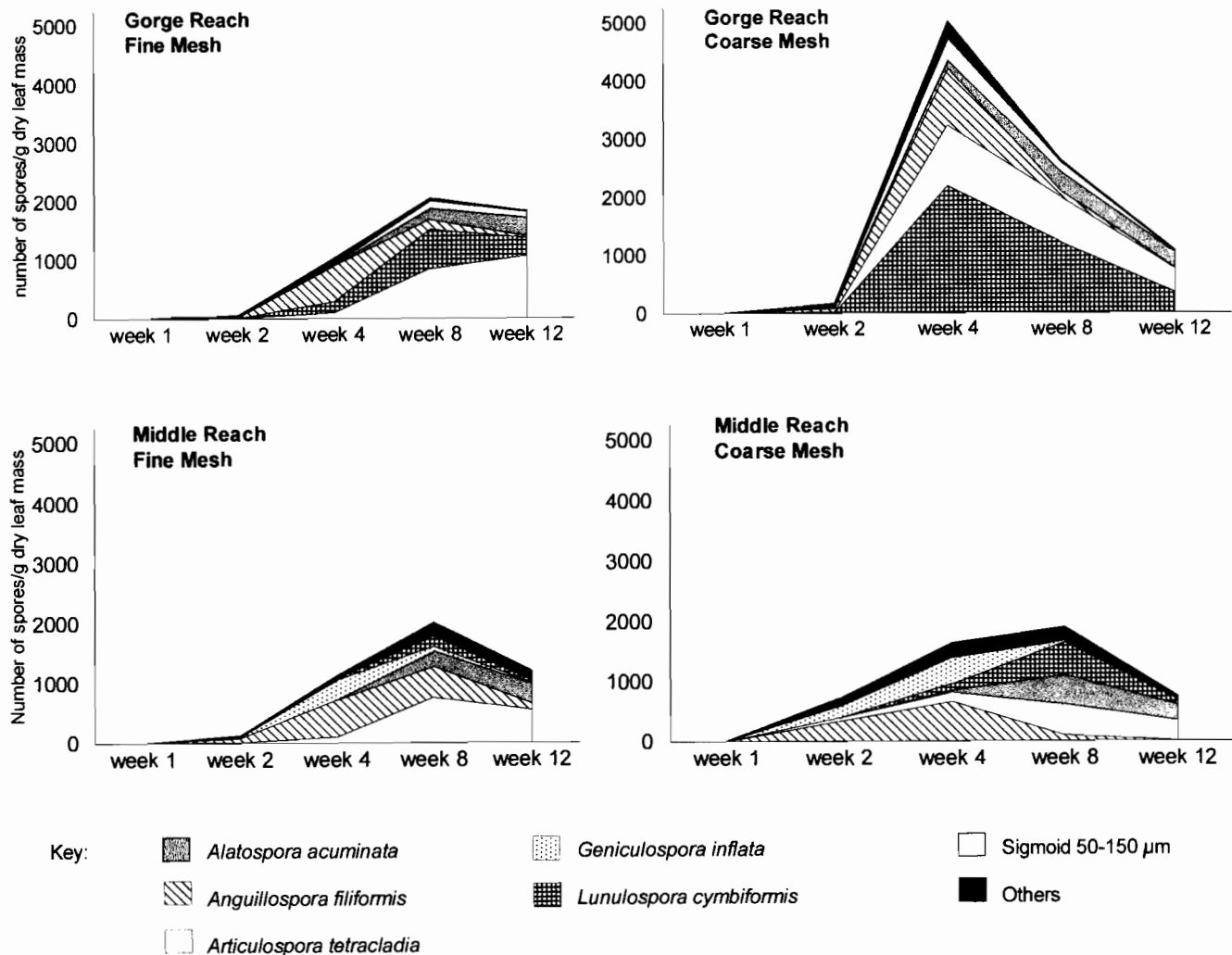


FIG. 3. Spore production over time and relative importance of important taxa of aquatic fungi at two sites in Catamaran Brook in summer 1995 (May 24 to Aug 15, 1995).

there were no consistently positive or negative differences between the Gorge site (close to logging area) and the Middle Reach site (remote from logging area). In the winter experiment, site no longer had a significant effect; in the following summer, all three measures of diversity were significantly influenced by site, but again, there were no consistently positive or negative differences between the two sites.

**Colonization patterns.**—Spore production per unit leaf mass varied significantly over time in all trials (ANOVA,  $P < 0.001$ , TABLE II). It reached a maximum between 4 and 8 (summer trials) or between 2 and 4 (fall trial) wk of immersion (FIGS. 3–5). In the summer trials, mesh size significantly affected spore production; it peaked earlier and was generally higher in coarse-mesh bags. Spore numbers were generally higher in the Gorge Reach than the Middle

Reach (FIGS. 3–5, TABLE III), but site was no longer a significant factor in summer 1996 (ANOVA,  $P = 0.95$ , TABLE II).

It is often difficult to recognize fungal colonization patterns due to extreme variability of spore production within and between trials. To facilitate this, relative abundances of all taxa are presented as kite diagrams in FIG. 8, and patterns are summarized in TABLE IV. Three main patterns are noted. Some taxa were only present, or had their highest abundance, very early in the colonization period; most arrived or peaked during the intermediate stages of leaf decay, and a few were characteristic of the latest stages (FIG. 8). Two species, *Lambdasporidium viridense* and *Tripospermum myrti*, were consistent early colonizers in all three trials; *Clavariopsis aquatica* was the only species that consistently peaked toward the end of all three trials.

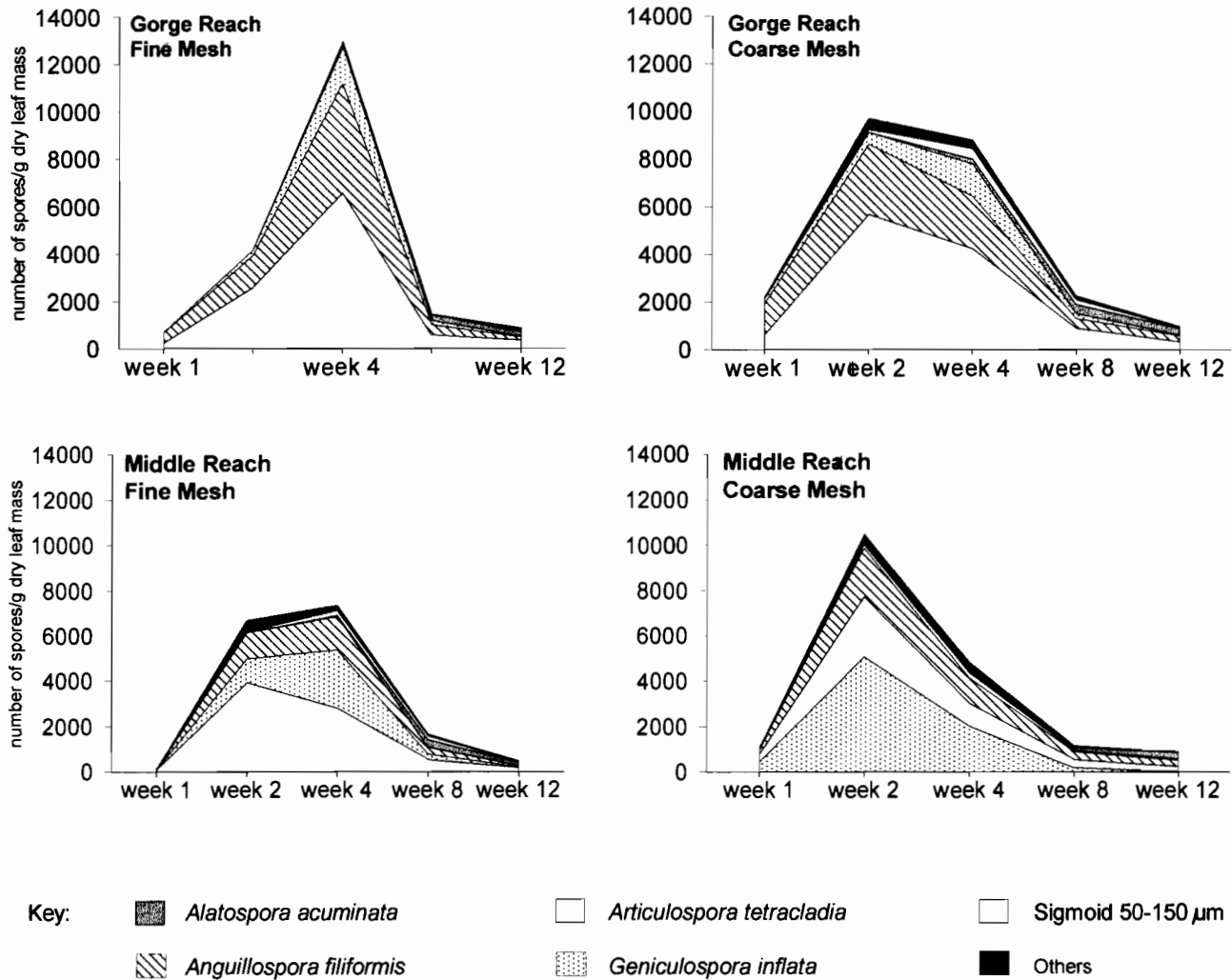


FIG. 4. Spore production over time and relative importance of important taxa of aquatic fungi at two sites in Catamaran Brook in fall 1995 (Sep 22 to Dec 14, 1995).

#### DISCUSSION

Due to the scarcity of reproductive structures, the fungal community on leaves decaying in streams cannot usually be identified to species (Bärlocher 1992b). A variety of methods, all based on inducing spore production on the leaf or on cultures isolated from the leaf, have been used (Shearer and Lane 1983). In recent years, aerating freshly collected leaves in distilled water and harvesting newly released spores on Millipore filters has become a favorite approach. Maximum numbers of spores produced under these conditions correlate both with maximum fungal biomass (as estimated by ergosterol measurements) and exponential decay rate coefficients (Gessner and Chauvet 1994, Maharning and Bärlocher 1996), and can therefore serve as indicators of the fungi's ecological contributions to the stream ecosystem. Maximum spore production rates in the current study ( $1.2\text{--}3.7$  spores  $\mu\text{g}^{-1}$  day $^{-1}$ ; TABLE III) fall with-

in the range of values reported to date (0.6–3, Bärlocher 1982; 4–7, Bärlocher et al 1995; 1–8, Gessner and Chauvet 1994; 0.2–0.8, Maharning and Bärlocher 1996), suggesting that Catamaran Brook provides favorable conditions for aquatic hyphomycetes. This is confirmed by the number of species: 35 species were identified during the fall 1995 trial, and 27 each in the two summer trials. In temperate streams, the highest cumulative numbers of fungal species during the breakdown of single substrates have generally been reported for *Alnus glutinosa* leaves decaying in softwater streams (17–24 species, Bärlocher et al 1995; 43 species, Gessner et al 1993; 22–42 species, Shearer and Webster 1985). Lower numbers have been found in hardwater streams. For example, the cumulative numbers from three substrates varied between 11–17 in two hardwater and from 21–33 species in two softwater streams (Bärlocher 1982). Extremely low species richness (2–11) was found in sev-

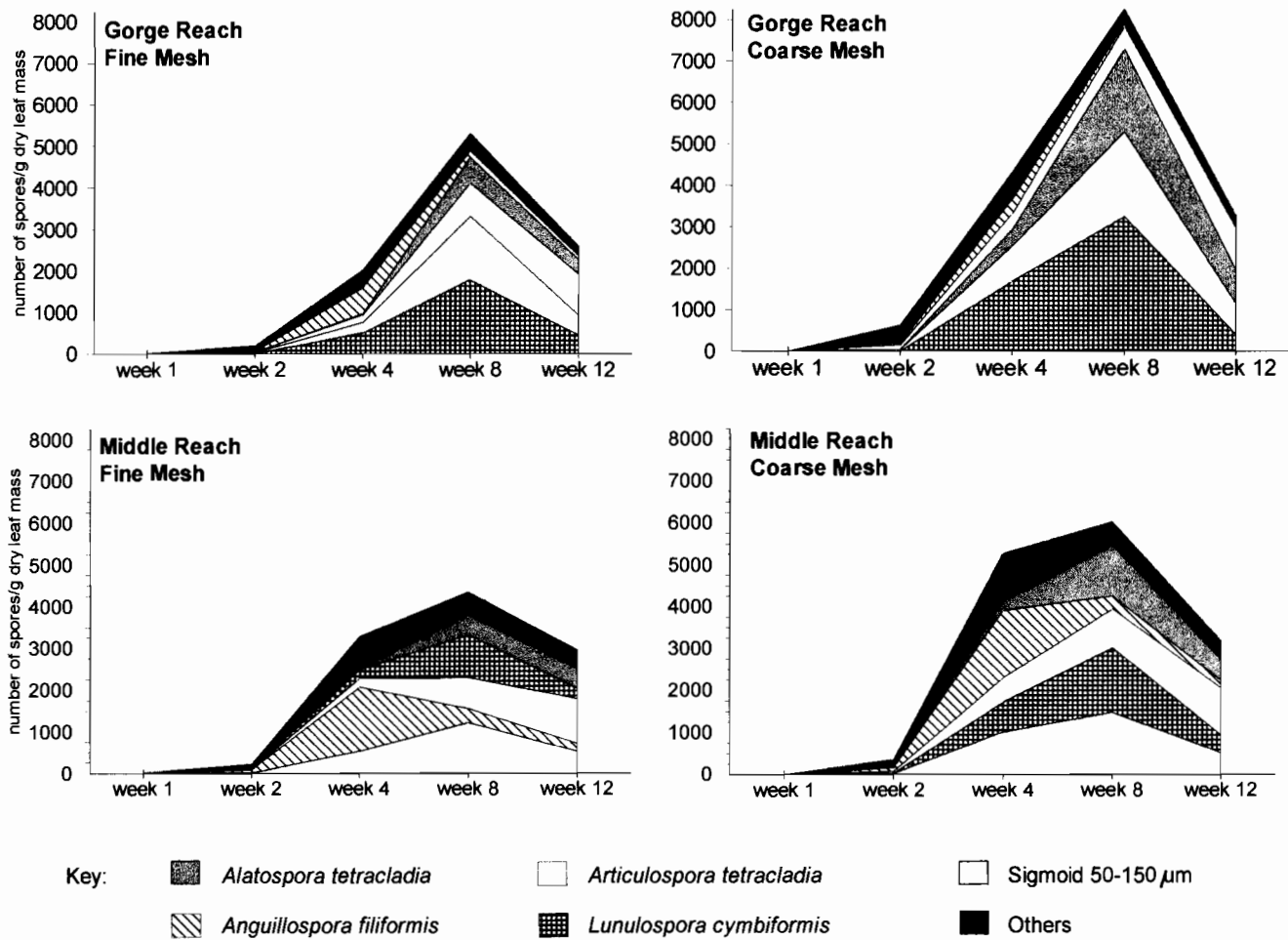


FIG. 5. Spore production over time and relative importance of important taxa of aquatic fungi at two sites in Catamaran Brook in summer 1996 (May 22 to Aug 14, 1996).

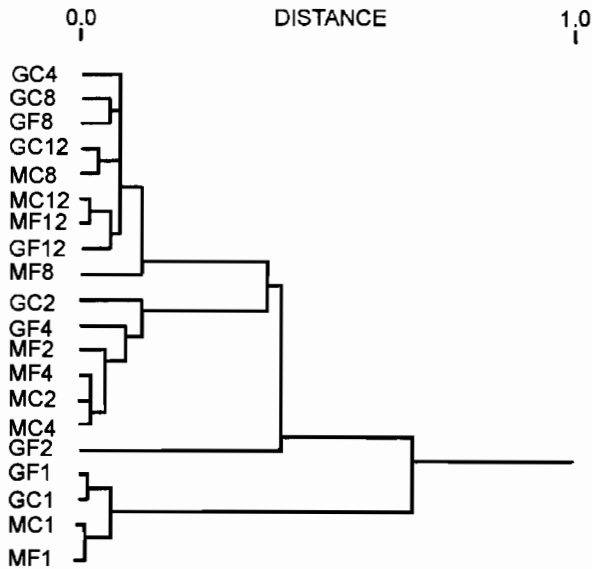
eral Alabama streams with very low nitrogen and phosphate levels (Suberkropp and Chauvet 1995). We conclude that Catamaran Brook has a diverse and active aquatic hyphomycete community; it is therefore well suited to study the impact of logging on decomposition processes.

Both spore production and overall species richness were higher in the fall than in the summer trials. This confirms the results from many other studies of temperate streams (Bärlocher 1992b). They generally reveal a distinct period, coinciding with leaf fall and falling water temperature, of increased vegetative growth and/or reproduction of aquatic hyphomycete communities. This is reflected by spore numbers carried in the water column; in the summer months, many species fall below detection thresholds. The seasonal cycling is less pronounced in streams bordered by conifers, where input of new substrates is more evenly spaced over the entire year (Bärlocher 1992b). Conversely, in a spring-fed stream with a constant temperature of 22 C, all species reacted in a

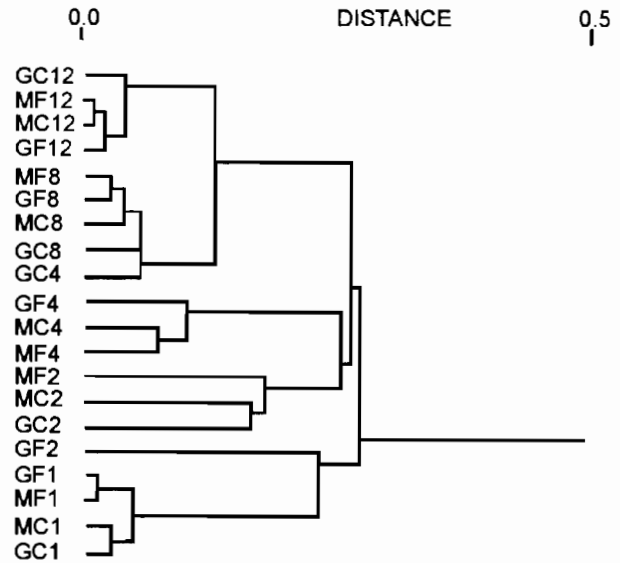
similar, predictable way to the autumnal leaf fall and the gradual disappearance of leaves (Akridge and Koehn 1987).

On substrates introduced into streams, fungal species richness is initially low, rises to a peak within a few wk, and subsequently remains stable or declines. Eventually, of course, the substrate will be exhausted or converted to fine particulate organic matter, and will no longer provide suitable conditions for any fungal species. Despite this overall pattern of entire communities, there is considerable variation of how individual species vary through the seasons. The most clear-cut factor generally seems to be temperature: species such as *Triscelophorus monosporus* and *Lunulospora curvula* have repeatedly been associated with warm water temperatures (Bärlocher 1992b). We did not observe *L. curvula*, but a related species, *L. cymbiformis*, did appear to be less common in the later stages of the fall trial than in the two summer trials. *Triscelophorus monosporus*, on the other hand, was more common in the later stages of fall 1995 than in

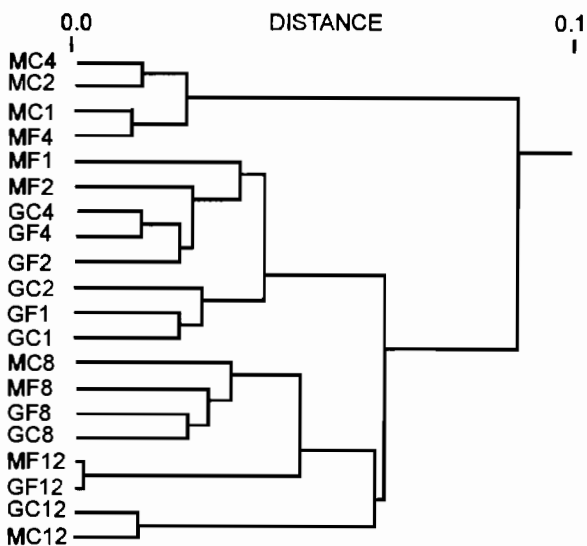
## SUMMER 1995



## SUMMER 1996



## FALL 1995



## WINTER 1995/1996

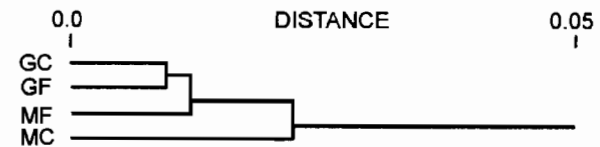


FIG. 6. Results of cluster analysis, examining similarity of fungal communities in the different study sites and on the different sample dates in Catamaran Brook, May 1995 to Aug 1996. G, M: Gorge, Middle Reach; C, F: coarse, fine mesh. Distance =  $(1 - \text{Pearson's correlation coefficient})$ .

summer 1996. However, it never was abundant. This sporadic appearance makes it more susceptible to random variability, which may hide real patterns or suggest spurious ones. Rare species are more likely to be noted when the overall numbers of spores are low (in mid-successional samples, the 4–6 most common species can account for over 99% of all conidia); not surprisingly, the rare species in our study (occurring 1–3 times per trial) were all observed either at the beginning or at the end of the trials. Only two occurred in all three full trials, *Lambdasporium viridense* and *Tripospermum myrti*. Both appeared in the

early samples. The preferred habitat of *T. myrti* may well be terrestrial; its disappearance in later stages may simply reflect its inability to compete in the stream environment. *Lambdasporium viridense* has been reported primarily from tropical streams (Marvanová 1997). This might explain why it was absent in middle and late samples of the fall trial; it does not explain the same behavior in the two summer trials.

The six most abundant species, which together accounted for nearly 95% of the total spores found, all tended to persist in the population over several

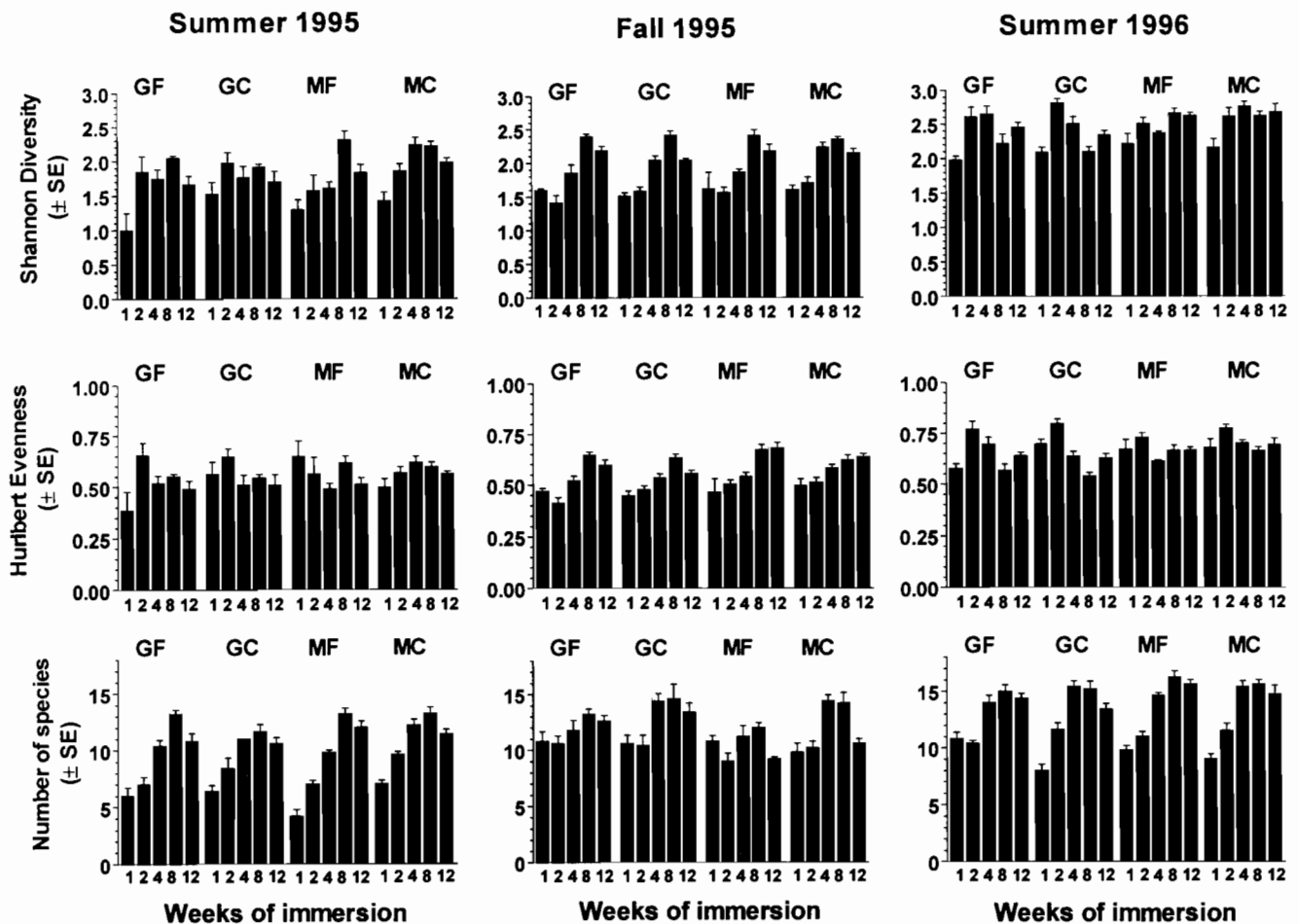


FIG. 7. Species diversity patterns over time and among trials (determined for individual leaves within each sample date and trial, and averaged, values are numbers  $\pm$  SE) for aquatic fungi in Catamaran Brook, May 1995 to Aug 1996.

weeks. Again, some appear to be more common in the earlier stages (e.g., *Anguillospora filiformis*, *Geniculospora inflata*), others in the later stages (e.g., *Articulospora tetracladia*). The question remains how stable such patterns are over several years or across several streams. In a review of 20 studies in temperate streams, 29 different fungal taxa reached the top five ranks at least once (Bärlocher 1992b), but there was considerable variability in the timing of their appearance. Only four species behaved fairly consistently in all studies. Two of them were either absent in our study (*L. curvula*) or never common (*Tetracladium marchalianum*). *Flagellospora curvula* generally declined in later stages. If the species designated as sigmoid 50–150  $\mu\text{m}$  in our study is indeed *F. curvula*, its pattern agrees more or less with these earlier studies, except during the summer 1996 trial. The fourth species, *Clavariopsis aquatica*, was reported to be common throughout the successions; in our study, it tended to increase in later stages.

**Logging effects.**—The high variability in abundance patterns, both within and between studies, limits the

use of such patterns of individual fungal species to evaluate the effects of disturbance. Differences in the fungal community between Gorge and Middle Reach were negligible. It is therefore appropriate to use the Middle Reach (distant from logging) as internal control to the Gorge site (close to logging). With the more comprehensive approach by cluster and principal component analyses, we established that length of immersion clearly dominated overall community patterns. This implies that disturbance cannot be evaluated by single samples from arbitrarily chosen successional stages and the strength of the time-related pattern may mask all but the most drastic of disturbance effects.

One of our objectives was to determine direct and indirect effects of logging on the fungal community. Among the indirect effects, its impact on leaf-shredding macroinvertebrates (which in turn may act as predators/competitors of aquatic hyphomycetes; Bärlocher 1980) is likely the most important one. To establish the effect under prelogging conditions, we used fine (excludes invertebrates) and coarse (allows

TABLE II. Probabilities values from ANOVA investigating effects of site (Gorge vs Middle), mesh size (fine vs coarse), or time of immersion (week) on various community structure variables in Catamaran Brook, NB, 1995 and 1996

Season/ effects	Sporulation		Evenness (v)	Richness
	(#/dry wt)	Diver- sity (h)		
Summer 1995				
Site	0.003	0.080	0.170	0.077
Mesh	0.002	0.011	0.409	0.001
Week	0.000	0.000	0.033	0.000
Fall 1995				
Site	0.008	0.106	0.001	0.001
Mesh	0.102	0.139	0.901	0.001
Week	0.000	0.000	0.000	0.000
Winter 95/96				
Site	0.086	0.084	0.261	0.405
Mesh	0.088	0.57	0.525	0.904
Week <sup>a</sup>	n/a	n/a	n/a	n/a
Summer 96				
Site	0.953	0.000	0.011	0.025
Mesh	0.000	0.219	0.073	0.398
Week	0.000	0.000	0.000	0.000

<sup>a</sup> Week could not be tested during the winter trial, since only one sample was collected.

macroinvertebrates) mesh bags. We expected decreased spore production and fungal species richness on leaves exposed to feeding invertebrates (Bärlocher 1980, Suberkropp and Wallace 1992). We did not find any consistent correlation between mesh size and any of the measures of fungal diversity or community patterns, although, contrary to expectations, spore production tended to be higher on leaves in coarse mesh bags than the fine mesh ones. One contributing factor may have been the presence of large numbers of black fly larvae settling on some of the fine-mesh bags during summer samples (Garnett 1998). Their filtering activity may have prevented some fungal spores from reaching the leaves. [Fungal-invertebrate relationships and their effect on decomposition rates will be more fully discussed in another paper (Garnett et al unpubl)]. Alternatively, material (including black fly larvae) accumulating on fine mesh bags may have impeded water flow through the bags, and biased the interpretation of invertebrate feeding effects.

We originally anticipated that logging would start in early 1996. This would have allowed a comparison of a preharvest (summer 1995) with a post harvest (summer 1996) trial. Unfortunately, the only logging activity that took place was some road building in late

TABLE III. Maximum number of spores released from individual leaves recovered from Catamaran Brook (spores mg<sup>-1</sup> day<sup>-1</sup> dry mass)

Reach	Mesh size	Winter			
		Summer 1995	Fall 1995	1995- 1996 <sup>a</sup>	Summer 1996
Gorge	Fine	383	1842	64	568
	Coarse	1471	3687	103	1212
Middle	Fine	210	1071	145	602
	Coarse	214	2469	148	848

<sup>a</sup> Only one sample was taken in the winter 1995-1996 experiment.

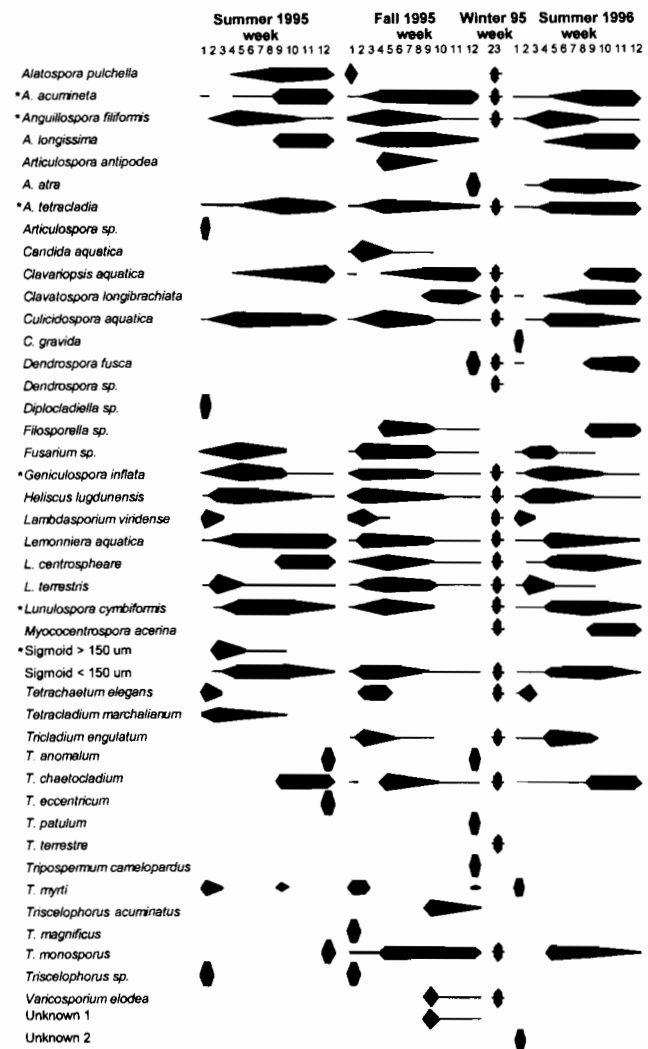


FIG. 8. Colonization patterns (relative abundance over time) for aquatic fungi in Catamaran Brook, May 1995 to Aug 1996. The six most abundant species are marked with \*.

TABLE IV. Colonization patterns of hyphomycetes on leaves in Catamaran Brook<sup>a</sup>

Highest at 1–2 wk	Early species Highest at 1–8 wk	Highest at 2–4 wk
<i>Alatospora pulchella</i> <sup>F95</sup>	<i>Anguillospora filiformis</i> <sup>F95</sup>	<i>Candida aquatica</i> <sup>F95</sup>
<i>Articulospora acuminata</i> <sup>S95</sup>	<i>Lemonniera centrosphaera</i> <sup>F95</sup>	<i>Fusarium</i> sp. <sup>S96</sup>
<i>Culicidospora gravida</i> <sup>S96</sup>	<i>Tetracladium marchalianum</i> <sup>S95</sup>	<i>Lemonniera terrestris</i> <sup>F95</sup>
<i>Diplocladiella</i> sp. <sup>S95</sup>		Sigmoid >150 <sup>S95</sup>
<i>Lambdasporium viridense</i> <sup>S95, F95, S96</sup>		<i>Tetrachaetum elegans</i> <sup>F95</sup>
<i>Tripospermum myrtil</i> <sup>S95, F95, S95</sup>		<i>Tricladium angulatum</i> <sup>F95</sup>
<i>Tetrachaetum elegans</i> <sup>S95, S96</sup>		
<i>Triscelophorus magnificus</i> <sup>F95</sup>		
<i>Triscelophorus</i> sp. <sup>F95</sup>		
Unknown 2 <sup>S96</sup>		
Highest at 2–8 wk	Middle species Highest at 4–8 wk	Highest at 4–12 wk
<i>Anguillospora filiformis</i> <sup>S95, S96</sup>	<i>Articulospora antipodea</i> <sup>F95</sup>	<i>Alatospora acuminata</i> <sup>F95</sup>
<i>A. longissima</i> <sup>F95</sup>	<i>Culicidospora aquatica</i> <sup>S95, S95</sup>	<i>A. pulchella</i> <sup>S95</sup>
<i>Articulospora tetracladia</i> <sup>F95</sup>	<i>Filosporella</i> sp. <sup>F95</sup>	<i>Articulospora atra</i> <sup>S96</sup>
<i>Culicidospora aquatica</i> <sup>F95</sup>	<i>Lemonniera aquatica</i> <sup>S96</sup>	<i>A. tetracladia</i> <sup>S95, S96</sup>
<i>Fusarium</i> sp. <sup>S95, F95</sup>	<i>Lunulospora cymbiformis</i> <sup>S95, S96</sup>	<i>Lemonniera aquatica</i> <sup>S95</sup>
<i>Geniculospora inflata</i> <sup>S95, F95, S96</sup>	Sigmoid 50–150 <sup>S95, S96</sup>	<i>L. centrosphaera</i> <sup>S96</sup>
<i>Heliscus lugdunensis</i> <sup>S96, F95, S95</sup>	<i>Tricladium angulatum</i> <sup>S96</sup>	<i>Triscelophorus monosporus</i> <sup>F95, S96</sup>
<i>Lemonniera aquatica</i> <sup>F95</sup>	<i>T. chaetocladium</i> <sup>F95</sup>	
<i>L. terrestris</i> <sup>F95</sup>		
<i>Lunulospora cymbiformis</i> <sup>F95</sup>		
Sigmoid 50–150 <sup>F95</sup>		
Highest at 8–12 wk	Late species Highest at 12 wk	
<i>Alatospora acuminata</i> <sup>S95, S96</sup>	<i>Articulospora atra</i> <sup>F95</sup>	
<i>Anguillospora longissima</i> <sup>S95, S96</sup>	<i>Dendrospora fusca</i> <sup>F95</sup>	
<i>Clavatospora longibrachiata</i> <sup>F95, S96</sup>	<i>Tricladium anomalum</i> <sup>S95, F95</sup>	
<i>Clavariopsis aquatica</i> <sup>S95, F95, S96</sup>	<i>T. eccentricum</i> <sup>S95</sup>	
<i>Dendrospora fusca</i> <sup>S96</sup>	<i>T. patulum</i> <sup>F95</sup>	
<i>Filosporella</i> sp. <sup>S96</sup>	<i>Triscelophorus monosporus</i> <sup>S95</sup>	
<i>Lemonniera centrosphaera</i> <sup>S95</sup>	<i>Tripospermum camelopardus</i> <sup>F95</sup>	
<i>Mycocentrospora acerina</i> <sup>S96</sup>		
<i>Triscelophorus accuminatus</i> <sup>F95</sup>		
<i>Tricladium chaetocladium</i> <sup>S95, S96</sup>		
<i>Varicosporium elodea</i> <sup>F95</sup>		
Unknown 1 <sup>F95</sup>		

<sup>a</sup> F95 = fall 95; S95 = summer 95; S96 = summer 96.

fall 1995, leading to a minor increased suspended sediment event in Nov. As discussed earlier, this did not appear to have any consistent effect on the fungal community in the subsequent trial. When timber harvest occurred (following termination of the present study), extremely high levels of suspended sediment were recorded in the impact (Gorge) site. Our results allow some speculation as to what changes due to logging might be revealed by looking at fungal succession on decomposing leaves. It seems clear that with the current state of knowledge we are unable to detect relatively subtle changes in the community,

such as those possibly relating to a small increase in suspended sediment in the stream. Anthropogenic disturbances which clearly damage fungal stream communities include organic pollution, coal mine effluents and heavy metal contamination (Bärlocher 1992b). Effects include reductions in species richness by 50–80% (Birmingham et al 1996, Maltby and Booth 1991, Raviraja et al 1998a). The primary effects of logging may include increased suspended sediment (which may blanket decaying substrates, and thereby deprive fungi of oxygen), increased temperature and light, reduced supply of leaves and oth-

er substrates, and as a consequence more algal and bacterial growth. Whether these changes will be drastic enough to significantly reduce the diversity and function of the fungal community of Catamaran Brook remains to be seen.

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