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Response of aquatic hyphomycete communities to enhanced stream retention in areas impacted by commercial forestry

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SUMMARY

1. Aquatic hyphomycetes are an important component of detritus processing in streams. Their response to enhanced stream retentiveness was tested by manipulating three streams located in Kielder Forest (northern England), a large plantation of exotic conifers, and two streams in Montagne Noire (south-west France) dominated by native broadleaf woodland. Treatment was by placement of logs or plastic litter traps into a 10–20 m stream section. Fungal spores were collected from stream water upstream and downstream of the treated sections over 1–2 years.

2. The average concentration of fungal spores in reference sections was nearly 10× greater in the French streams than in the English streams. The number of hyphomycete species was also higher in the French streams. These differences between regions were probably a consequence of the much lower standing stock and diversity of leaf litter in the English streams.

3. Despite these large regional differences, the treatment had a clear effect in all streams. Detrital standing stocks were enhanced in treated sections by up to 90% in French streams and 70% in English streams.

4. Mean spore density below treated sections increased by 1.8–14.8% in French streams and 10.2–28.9% in the naturally less retentive English streams. The number of fungal species increased significantly below the treated sections of the English streams, although not the French ones.

5. In biologically impoverished plantation streams, input of woody debris can increase detritus retention and enhance hyphomycete diversity and productivity. This may have consequent benefits for detritus processing and macroinvertebrate production.

Keywords: aquatic fungi, forest management, leaf litter, stream retentiveness, woody debris

Introduction

During the twentieth century, large areas of the U.K. were converted from open pasture to commercial forestry. Exotic conifers dominated this planting regime to the extent that they now account for over 60% of the 24 000 km^2 of woodland in Britain (Forestry Commission, 1998). Before the 1990s, most of

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this planting was in upland areas previously dominated by moorland and low-intensity grazing. These areas are often characterised by numerous small streams, where alteration from an open to a densely wooded habitat can bring about changes in hydrology, sedimentation, temperature and water chemistry (e.g. Hornung & Newson, 1986; Ormerod, Donald & Brown, 1989; Weatherley & Ormerod, 1990; Ormerod *et al.*, 1993), with an inevitable effect upon their biota.

Afforestation has an energetic impact upon upland streams by increasing shading and consequently suppressing primary productivity (Friberg, 1997). Forested rivers support relatively little primary production and depend upon allochthonous detritus for their major energy source (Webster & Meyer, 1997). Conifer needles are, however, of poor nutritional quality compared with many broadleaf species (Webster & Benfield, 1986). They possess a thick waxy cuticle and contain tannins that impede microbial conditioning, resulting in slow rates of decomposition (Sedell, Triska & Triska, 1975; Bärlocher, Kendrick & Michaelides, 1978) and poor food quality for invertebrate detritivores (Iversen, 1974; Friberg & Jacobsen, 1994). If, however, they are retained within the stream channel for several months, their nutritional quality is enhanced and they can support high microbial and invertebrate abundance (Sedell *et al.*, 1975; Bärlocher & Oertli, 1978; Grafius & Anderson, 1980; Bärlocher, 1982).

The most efficient retention structures in forested streams are pieces of dead wood (DW), in the form of branches, twigs and occasionally entire trees that fall into the channel (Bilby & Likens, 1980; Trotter, 1990). Where a formerly open catchment has been forested for commercial harvest, however, retention generally remains low because trees are removed before reaching the stage at which branches drop. Such streams therefore retain the low retention capacity of moorland streams (Cariss & Dobson, 1997). For these reasons, enhancing the retention capacity of river channels has been proposed as a management strategy for rivers impacted by forestry (Dobson *et al.*, 1995). Ideally, this would be in the form of buffer zones removed from commercial activity (Forestry Commission, 1993; Dobson & Cariss, 1999).

Research into interactions between coarse particulate organic matter (CPOM), retention and biota has concentrated upon macroinvertebrates (e.g. Prochazka, Stewart & Davies, 1991). Other organisms are, however, crucial in detritus processing in streams. Among these are hyphomycete fungi, diverse microfungi which are important decomposers as well as crucial agents in the conditioning of leaf litter to improve its nutritional quality for invertebrate detritivores (Bärlocher & Kendrick, 1976). Microfungi can account for up to 17% of detrital leaf mass and their annual production, determined on a stream area basis, may be in the same general range as the production of bacteria or macroinvertebrates (Gessner, 1997; Suberkropp, 1997). Conifer needles can support a substantial number of aquatic hyphomycete species, equal to that of some broadleaf species (Bärlocher, 1992), but colonisation of this substrate is quite slow, requiring long periods of submersion.

The response of aquatic hyphomycetes to experimental elevation of CPOM levels is unknown. Hyphomycetes allocate much of their production to the formation of asexual reproductive spores (conidia), the densities of which can rise to several thousands per litre of stream water after peak leaf fall in autumn (Bärlocher, 1992). Despite this, natural aggregations of CPOM apparently have little effect on overall conidial densities, although the relative abundance of some species is altered (Thomas, Chilvers & Norris, 1991a).

The aim of this study was to examine the effect of artificially enhanced detritus retention on conidial production and diversity of aquatic hyphomycete communities in forested streams. Although inspired by the high impact forestry practised widely in the U.K. and elsewhere in north-west Europe, we wished to determine the extent to which any patterns observed could be generalised to other forestry systems. Therefore, we repeated the study in a region typical of the moderately low intensity forestry common in upland regions of France, where native broadleaf woodlands dominate river valleys and conifer plantations are confined to higher slopes and hill tops. This study provided an opportunity to test whether this landscape-level disturbance altered aquatic hyphomycete communities, and therefore to provide guidance for management strategies that may maintain or enhance hyphomycete diversity and overall river health.

Methods

Study sites

The experiment was carried out in two areas differing in forestry practice. Kielder Forest (northern England) is the largest single area of conifer plantation in the U.K., covering *c.* 475 km^2 with an altitudinal range of 150–500 m a.s.l. The plantation is intensively managed, planted mainly with Sitka spruce [*Picea sitchensis* (Bong.) Carrière], but with Norway spruce [*P. abies* (L.) Karsten] common in valley bottoms. The area was dominated by rough grazing pasture until afforestation, which began in 1926 and peaked between 1946 and 1960, when 200 km^2 were planted (Hibberd, 1985). In most cases, buffer zones were not incorporated into the planting regime, and the commercial species extended to the banks of the rivers. Montagne Noire (south-western France) is dominated by mixed broadleaf woodland of *c.* 1450 km^2, with an altitudinal range of 250–1211 m a.s.l. During the twentieth century, the forest was converted into a commercial production of beech (*Fagus sylvatica* L.) and Norway spruce, and the process accelerated in the 1960s when the National Forest Fund (Fond Forestier National) began to promote conifer plantations. The landscape is dominated by even-aged forest stands, but in some areas more traditional forest management practices are applied. For instance, several areas comprise oak coppice-with-beech standards, where natural regenerating vegetation is preserved. Streams are supplied with leaves and woody debris from oaks (*Quercus robur* L., *Q. humilis* Miller ssp. *humilis, Q. petraea* Liebl.), beech, hazel (*Corylus avellana* L.) and willow (*Salix* sp.).

Five permanent first-order streams were used in this study (Table 1). Capon Burn and Kittythirst, in Kielder Forest, flow through stands of mature Norway spruce, with Sitka spruce predominant away from valley bottoms. Steep Sike, also in Kielder Forest, flows through an area planted with Sitka spruce but has a riparian zone of alder [*Alnus glutinosa* (L.) Gaertn.]. Dental and Fraïssègne, on the southern side of the Montagne Noire, flow through the coppice-with-standards forest described above, their well-shading riparian vegetation composed predominantly of oak, hazel and beech. Temperature was followed using dataloggers over the study period (Table 1). Conductivity and pH were determined at each sampling date. Stream width was averaged on five measurements along the stream sections. Substratum types within the stream sections were evaluated visually and ranked according to their relative importance. Macroinvertebrate assemblages (Pretty, 2000) indicated a good quality of water in all streams.

Study design

Kielder Forest. In each stream a 20-m experimental length was delineated, of which the upstream 10 m was the reference section and the downstream 10 m was the treated section. Each stretch chosen was representative of the stream over a larger reach in terms of width, depth, flow, substrate and riparian vegetation. Retention immediately prior to treatment was compared between reference and treated sections by sampling benthic CPOM and DW standing stocks using five Surber samples (area 0.0625 m^2, mesh size 250 μm) taken from arbitrarily selected points within each section. The woody component (DW) included sticks and bark fragments but branches (wood >4 cm

Table 1 Physical and chemical characteristics of the streams

	Kielder Forest			Montagne Noire	
	Steep Sike	Kittythirst	Capon Burn	Dental	Fraïssègne
Latitude	55°11′28″N	55°15′31″N	55°12′55″N	43°25′28″N	43°25′15″N
Longitude	2°36′04″W	2°37′06″W	2°34′15″W	2°14′11″E	2°14′00″E
Altitude (m) a.s.l.	240	230	210	715	705
Width (m)	2.2	1.6	1.8	0.9	1.0
Temperature (°C)	1.4–12.2	5–11	2.1–10.8	2.2–16.9	0–20.6
pH	3.9–6.6	7.2–8.3	4.2–7.6	6.0–6.8	6.1–6.8
Conductivity (μS cm^{-1})	40–71	178–267	45–136	19–29	19–34
Substratum	Boulder, gravel	Gravel, sand	Boulder, gravel	Boulder, gravel, sand	Boulder, gravel, sand
Riparian trees	*A. glutinosa*, *P. sitchensis*	*P. sitchensis*, *P. abies*	*P. sitchensis*, *P. abies*	*Q. robur*, *C. avellana*, *Q. petraea*, *F. sylvatica*	*Q. robur*, *Q. petraea*, *F. sylvatica*, *C. avellana*

diameter) were excluded. The CPOM fraction was determined by washing each sample through a 1-mm mesh sieve. The CPOM and DW were separately dried to a constant weight (50 °C) and subsamples were combusted at 550 °C to obtain an ash free dry mass (AFDM).

In the treated section of all streams, retention was enhanced by securing 10 logs (each 1 m long, 10 cm diameter), perpendicular to the stream axis at approximately 1-m intervals. Treatments were carried out on 10 April 1997 in Capon Burn and Kittythirst, and on 29 October 1997 in Steep Sike. Logs were derived from Sitka spruce harvested locally.

Following treatment, mass of CPOM and DW was sampled approximately seasonally (October 1997; January, May, August and November 1998; April 1999). Five Surber samples were taken from the reference section and five from immediately downstream of arbitrarily chosen logs in the treated section. All samples were sieved, dried and combusted in the same manner as described above.

Hyphomycete spores were collected from the downstream end of each reference section immediately before treatment. Following treatments, samples were collected from the downstream end of each reference and treated section at each stream on the same dates as detritus sampling. Three replicate samples were taken on each occasion. Samples of spores were collected by filtering on site 500 mL of stream water through a Whatman cellulose nitrate membrane filter (5 μm porosity) (Whatman International Ltd., Maidstone, UK). The filters were fixed and stained with a 60% lactic acid and 0.1% Trypan blue solution (Iqbal & Webster, 1973). All filters were examined microscopically at 200× magnification and spores present were counted and identified to species. Conidial density (number of spores per litre of stream water) and species richness (number of species per stream section) were determined. An index of conidial evenness, the V′ equitability index (Hurlbert, 1971), was calculated from the Shannon–Wiener function (Shannon & Weaver, 1949) according to Krebs (1989).

Montagne Noire. Sampling and treatments were the same in Montagne Noire streams as in Kielder streams, with the following exceptions. Logs used for treatment were beech, derived locally. In Fraïssègne, the treated section was 20 m in length and instead of 10 logs, 20 smaller structures, each around 20 cm long, were placed at a density of 1 m^{-2}. These comprised 10 pieces of wood cut from the larger logs of the type used in other streams, interspersed with 10 litter traps made from steel poles and plastic mesh (Dobson, 1991). The experimental design at Dental was the same as that used in Kielder Forest. Treatment in Montagne Noire streams was carried out on 15 April 1998, following collection of premanipulation samples, and detritus was sampled on three further occasions (June 1998, October 1998, June 1999). In Dental, samples were taken adjacent to logs, as in Kielder Forest; in Fraïssègne, they were taken from around randomly chosen log pieces and traps.

The number of replicate filtered samples and the filtered volume at Montagne Noire streams were 5 and 100 mL, respectively. The differences in these values between regions were because of the overall higher density of spores and fine particulate organic matter (FPOM) on filters in Montagne Noire relative to Kielder Forest.

Calculation of CPOM and DW standing stocks

Total mass of CPOM and DW in each reference section was estimated by extrapolating Surber sample contents over the entire section. The treatment was estimated to enhance detritus standing stocks over approximately 20% of the treated section (M. Dobson & J. Pretty, unpublished), leaving the remaining 80% unaffected (i.e. the same as the reference section). Samples taken from the treated section were therefore used to estimate the mass of detritus over 20% of the treated section, and those from the appropriate reference section were used to estimate the remaining 80%. In this way, we were able to estimate the total mass of detritus over the entire treated section. Note however, that estimates of standing stocks in treated sections are probably conservative because the treatment samples were only partially within the aggregations created by the logs, as detritus beneath and directly upstream from the logs could not be effectively sampled with a Surber net.

Statistical analyses

The Kielder and Montagne Noire studies were treated separately in the analyses. The main comparison in each case was between reference and treated sections within a stream. Between streams, comparisons are only possible to a limited extent as slight differences in treatment protocol occurred between some streams.

Before treatment, CPOM and DW standing stocks were compared between reference and treated sections using a two-way analysis of variance on log $(x + 1)$ transformed data with 'Treatment' (i.e. reference or treated) and 'Stream' as factors. After treatment, the same analyses were carried out with 'Time' as an additional factor.

Because individual filter samples could not be considered as true replicates for each 'Treatment /Stream/Time' combination, these data were pooled. Conidial densities were tested for normality distribution, and those not normally distributed were $\log_{10}$ transformed. Densities were compared using paired *t*-tests on values from the reference and treated sections. This analysis was carried out for total conidial densities and for densities of each individual species. Species richness and equitability were compared using paired *t*-tests repeated in the same way as for conidial density.

Results

Kielder forest

Standing stocks of CPOM ($P = 0.917$) or DW ($P = 0.237$) did not differ between reference and pretreated sections in any of the streams (Table 2). Dead Wood was almost absent from all rivers. Moreover, conidial density, species richness and diversity from pretreated sections were in the range of values found in reference sections, except in Capon Burn where species richness was low (Fig. 1). Treatment resulted in significant ($P < 0.001$) increases of both CPOM and DW standing stocks in all treatments and differences increased over time. The CPOM in the treated section had increased by 51% in Kittythirst, 69% in Steep Sike and 71% in Capon Burn by the final sampling date. Increases in DW (other than the added logs) occurred but percentage changes were not calculated because DW was only continually present in treated sections.

A total of 38 hyphomycete species was recorded across the three Kielder streams, and the number of species from each sampling period ranged from 2 to 17 (Appendix 1). The number of species occurring downstream of treated sections was significantly higher than in reference sections (Table 3, Fig. 1). Steep Sike exhibited the highest and most consistent differences in species richness between sections, averaging greater than three extra species in the treated section. Fungal equitability was, however, not affected by the treatment.

Conidial densities averaged 137 L^{-1} (range 9–928), with a seasonal pattern of minimum densities generally occurring in spring and maxima in autumn (Fig. 1). Conidial densities in treated sections were significantly higher than reference sections (Table 3). The average increase over the course of the study was 10.2, 17.6 and 28.9% in Steep Sike, Kittythirst and Capon Burn, respectively. The fungal community was predominated by three species (*Flagellospora curvula* Ingold, *Articulospora tetracladia* Ingold and *Alatospora acuminata* Ingold), which accounted for almost 60% of the total conidial production from the three streams during the study. Community composition differed between streams, with Steep Sike and Capon Burn exhibiting a similar species distribution that contrasted with that of Kittythirst.

Montagne Noire

No significant pretreatment differences were found in standing stocks of CPOM ($P = 0.498$) or DW

Table 2 Coarse particulate organic matter (CPOM) and dead wood (DW) standing stocks (g dm^{-2}) before and after treatment in the upstream, reference and downstream, treated sections

			Mean (SE)	
	Type	Region	Reference	Treated
Pre-treatment	CPOM	Kielder (n = 6)	0.26 (0.08)	0.24 (0.06)
		Montagne Noire (n = 4)	0.87 (0.11)	0.76 (0.08)
	DW	Kielder (n = 6)	0.03 (0.02)	0.00 (0.00)
		Montagne Noire (n = 4)	0.22 (0.14)	0.01 (0.05)
Treatment	CPOM	Kielder (n = 19)	0.29 (0.02)	0.44 (0.03)
		Montagne Noire (n = 6)	0.82 (0.12)	1.26 (0.28)
	DW	Kielder (n = 19)	0.02 (0.01)	0.15 (0.02)
		Montagne Noire (n = 6)	0.15 (0.04)	0.46 (0.10)

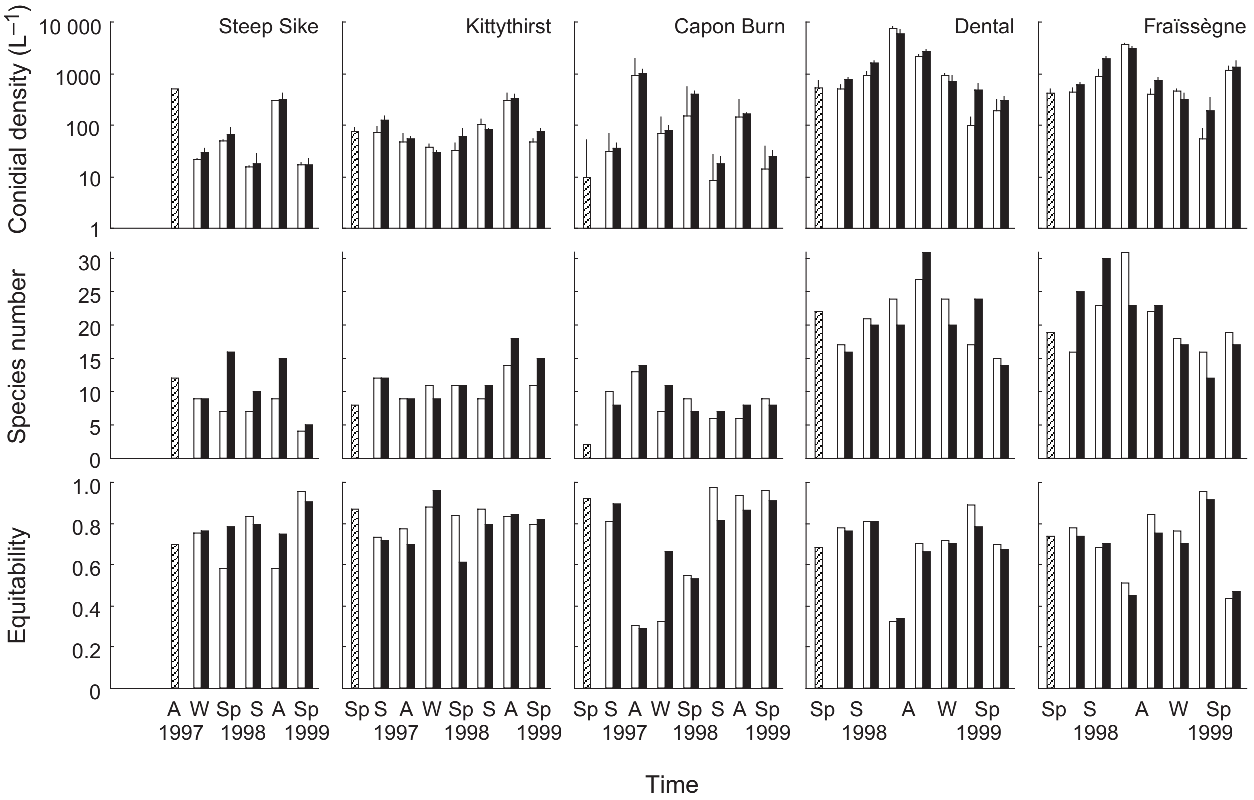

Fig. 1 Conidial density (log scale; mean + SE), species number and equitability of the fungal communities in pretreated (▨), reference (☐) and treated (■) sections of the streams in Kielder Forest (Steep Sike, Kittythirst, Capon Burn) and Montagne Noire (Dental, Fraïssègne).

Table 3 Paired *t*-test of hyphomycete community data between upstream, reference and downstream, treated sections. The *t*-values refer to 'Reference–Treated' differences

	Kielder (n = 19)		Montagne Noire (n = 14)	
	t	P-value	t	P-value
Conidial density	–3.609	0.002	–2.442	0.029
Species number	–2.379	0.028	–0.108	0.915
Equitability	–0.204	0.840	2.777	0.016

($P = 0.500$) between reference and treated sections in either of the streams (Table 2). Dead wood was present in reference sections of both streams throughout the study. Conidial density, species richness and diversity in treated sections were equivalent to those in corresponding reference sections (Fig. 1). Treatment led to significant increases in CPOM and DW standing stocks ($P < 0.001$), and the increases in CPOM built up over time. By the end of the study, the total mass of CPOM in the treated sections increased by 30% in Dental and 91% in Fraïssègne and, DW increased by 187 and 231%, respectively.

A total of 55 hyphomycete species was recorded from the two streams, and the number of species from each sampling period ranged from 12 to 31 (Appendix 1). There was no consistent trend in species richness between reference and treated sections. Fungal equitability was, however, significantly lower in the treated than in the reference sections (Table 3, Fig. 1).

Conidial densities averaged 1292 L^{-1} (range 54–7650), and showed clear seasonal patterns, with minimum densities generally occurring in spring and maxima in autumn (Fig. 1). There was a significant increase in conidial densities in treated sections (Table 3), the average increase over the course of the study being 1.8% in Dental and 14.8% in Fraïssègne *Flagellospora curvula* accounted for 45% of conidial densities, and three species (*A. tetracladia*, *Mycocentrospora* sp. 1 cf. *angulata* Petersen and *A. acuminata*) contributed an additional 22% in the two streams. The other species accounted for <5% of the total conidial densities and generally occurred with similar abundance and seasonal patterns in both streams. Conidia of *Tricladium chaetocladium* Ingold and *A. tetracladia* were found in significantly ($P < 0.05$) higher numbers in treated sections.

Discussion

This study clearly showed that aquatic hyphomycetes respond to changes in CPOM and/or DW biomass in river channels. Although only rough estimates of CPOM and DW were used, our findings suggest clear enhancement of retention on a stream section basis. Addition of logs into streams in Kielder Forest resulted in a significant increase in conidial densities and species richness. In Montagne Noire the effect was much less marked (i.e. densities increased but not species richness), probably a consequence of the greater natural standing stocks of CPOM in these rivers.

Increases in conidial density downstream of treatments were surprisingly large. Half-life distances of conidial drift for three aquatic hyphomycete species have been estimated at about 0.7–0.8 km (Thomas, Chilvers & Norris, 1991b). Therefore, of the conidia passing the reference section sampling point, around 99% would still have been in transit through the treated section. The average increase in conidial density was, however, 10–29% in four of the five streams, demonstrating that densities of some species could be enhanced by increases in detrital standing stock over a very short distance. Thomas *et al*. (1991a) reported that, while there was no significant change in total density of aquatic hyphomycete conidia below a natural debris dam in an Australian stream, the density of one species (*T. chaetocladium*) increased significantly. This species was also one that showed the highest increase below the treated sections in Montagne Noire streams.

Two species whose sporulation was stimulated by the treatment (*A. tetracladia* and *T. chaetocladium*) have sexual states, a trait known in <10% of the species of aquatic hyphomycete (Webster, 1992). These species are frequently found on submerged wood, which may be used as habitat and nutritional resource, as well as a substrate for sexual reproduction (Shearer, 1992). Indeed, the long persistence of wood and associated habitat stability may promote the development of sexual states (Shearer, 1992). Moreover, large pieces of DW may favour colonisation by a higher number of species (Swift, 1976; Sanders & Anderson, 1979). It is impossible to determine whether the increase in sporulation and the presence of some species observed in the present study is a direct effect of the DW and CPOM retained in the treated section or, an effect of the wooden logs used as experimental retention structures. These logs were, however, cut from the locally dominant tree species and may have effectively mimicked the woody litter which naturally falls into the streams. In addition to the two species above, eight species *(Flabellospora acuminata* Descals, *Lemonniera centrosphaera* Marvanová, *Lunulospora curvula* Ingold, *Mycocentrospora acerina* (Hartig) Deighton, *Tricellula aquatica* Webster, *Tricladium caudatum* Kuzuha, *Tripospermum prolongatum* Sinclair & Morgan-Jones *and Triscelophorus konajensis* Sridhar & Kaveriappa; Appendix 1) were recorded in the treated sections but not in the reference ones, which could have also indicated a positive reponse to manipulation. Two of these (*L. curvula*, *M. acerina*) are reported to be predominant among the wood-colonising species of aquatic hyphomycete (Shearer, 1992). All eight species however, accounted for very low proportions (<0.1%) of the total stream conidial production so that the manipulation effect was not significant for any of these species. They nevertheless contributed to the increase in species richness observed below the treated sections.

The streams of the two regions exhibited marked differences in conidial densities and species richness of aquatic hyphomycetes. Conidial density, in particular, was strikingly different; in Kielder reference sections, densities were almost one order of magnitude lower than Montagne Noire (Fig. 1). A biogeographical explanation for these differences is unlikely, as hyphomycetes are extremely good dispersers and many species are global in distribution, being limited by local conditions rather than geographical barriers (Webster & Descals, 1981; Wood-Eggenschwiler & Bärlocher, 1985). Furthermore, it was not simply a case of poorer litter quality in Kielder, because a similar pattern was observed in Steep Sike (alder dominated) to that in the spruce dominated rivers. These differences may at least partially be the result of differences in retention or diversity of leaf litter inputs between the streams in the two areas, although differences between regions in water chemistry and temperature regime are also probably important factors affecting the hyphomycete communities.

The seasonal patterns and the high conidial densities and species richness found in the Montagne Noire streams were consistent with those observed for temperate, soft-water, streams flowing through broadleaf forests (Bärlocher & Rosset, 1981; Shearer & Webster, 1985; Chauvet, 1992; Gönczöl, Révay & Csontos, 1999). The abundance of leaf litter entering these streams and its variety in terms of quality and input timing make them optimal substrata for a large pool of fungal species. Although aquatic hyphomycetes apparently lack specificity with regard to the type of leaf litter, some quantitative differences in species occurrence have been observed on different leaf substrata, for example, when comparing rapidly decomposing with slow-decomposing leaf species (Suberkropp, 1992). Such substratum preferences indicate that a wide range of leaf litter quality may support higher number of fungal species than a limited variety of leaf species (Bärlocher, 1992).

Debris dams clearly enhanced conidial density and affected the composition of aquatic hyphomycete communities. Natural inputs from riparian trees that are allowed to mature would almost certainly have the same effect as the artificial treatment used here. Forest management practices which involve removal of riparian vegetation, and of DW inputs into river channels, will result in reduced production and impoverished fungal communities. The removal of DW is also detrimental to stream channel stability, the dynamics of particulate organic matter and the hydraulic heterogeneity of streams (Bilby, 1984; Gurnell, Gregory & Petts, 1995; Maridet *et al*., 1995; Piégay & Gurnell, 1997). Planting a buffer zone of broadleaf trees along streams has been proposed as a mechanism to stabilise and enhance the productivity of coniferous woodland streams (Dobson *et al*., 1995). Our results suggest that, even in the absence of such a modification, fungal productivity and diversity of streams bordered by coniferous plantations may be substantially improved by simply allowing riparian vegetation to remain intact. The removal of DW should be kept to a minimum and the input of wood from riparian trees encouraged. Ideally this should be the result of natural processes, but our study shows that this can be substituted/supplemented by anthropogenic inputs when riparian trees are scarce or absent. Whilst the enhancement of hyphomycete communities is normally of little concern to river managers, these organisms play a major role in detritus processing and are important in the nutrition of many invertebrates. Therefore, management that promotes effective detritus retention may have wider benefits to stream biota than simply enhancing hyphomycete assemblages. Even in the French streams studied, hyphomycetes showed a positive response to elevated retention, albeit generally lower than in Kielder streams. Despite undergoing low intensity management and being based upon native species, these streams could be affected detrimentally by forestry practice if harvesting for timber results in a loss of mature or senescent trees. In all forest plantations, the optimum management to maintain or enhance the integrity of streams should incorporate a buffer zone, removed from the commercial sphere, in the riparian area. Enhancing the diversity of leaf litter inputs, by encouraging a variety of different riparian tree species, would further enhance hyphomycete production and diversity.

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Appendix 1 The total number of aquatic hyphomycete species identified in the five streams as conidia collected upstream (u) and downstream (d) of the manipulated reach, (?) indicates an uncertain species or genus identification

	Kielder			Montagne Noire	
Species	Steep Sike	Kittythirst	Capon Burn	Dental	Fraïssègne
Alatospora acuminata Ingold	ud	ud	ud	ud	ud
Alatospora flagellata (Gönczöl) Marvanová	d			ud	ud
Alatospora pulchella Marvanová	ud	ud	ud	ud	ud
Anguillospora crassa Ingold	ud	d	u	ud	ud
Anguillospora?curvula Iqbal		d		ud	ud
Anguillospora filiformis Greathead				ud	ud
Anguillospora?furtiva Descals & Marvanová	ud	d	ud		
Anguillospora longissima (Sacc. & Sid.) Ingold	ud	ud	ud	ud	ud
Anguillospora rosea Descals & Marvanová	d	u	d	ud	ud
?*Arbusculina moniliformis* (Descals) Marvanová & Descals		ud	d		
Articulospora atra Descals			u	ud	d
Articulospora tetracladia Ingold	ud	ud	ud	ud	ud
Casaresia sphagnorum Fragoso				ud	u
Clavariopsis aquatica de Wildeman		ud	ud	ud	ud
Clavatospora longibrachiata (Ingold) Marvanová & S. Nilsson	ud	ud		ud	ud
Crucella subtilis Marvanová & Suberkropp				ud	ud
Culicidospora aquatica R.H. Petersen		ud		ud	ud
Culicidospora gravida R.H. Petersen		ud		d	ud
Dendrospora?nana Descals & Webster				ud	ud
Dendrospora erecta Ingold				ud	d
Dendrospora fusca Descals & Webster				u	u
Dendrospora tenella Descals & Webster				u	d

Appendix (Continued)

Species	Kielder			Montagne Noire	
	Steep Sike	Kittythirst	Capon Burn	Dental	Fraïssègne
Dwayaangam cornuta Descals	d	u	d		
Flabellospora acuminata Descals				d	d
Flagellospora curvula Ingold	ud	ud	ud	ud	ud
Fontanospora?eccentrica (R.H. Petersen) Dyko	ud				
Geniculospora inflata (Ingold) S. Nilsson	ud			ud	u
Goniopila monticola (Dyko) Marvanová & Descals				ud	ud
Gyoerffyella rotula (von Höhnel) Marvanová					u
Heliscella stellata (Ingold & Cox) Marvanová & S. Nilsson	d	u	d	ud	ud
Heliscina campanulata Marvanová				ud	ud
Heliscus lugdunensis Saccardo & Théry	ud	ud	ud	ud	ud
Isthmotricladia?britannica Descals in Descals & Webster	ud	ud	ud	ud	ud
Lemonniera aquatica de Wildeman				u	ud
Lemonniera centrosphaera Marvanová					d
Lemonniera cornuta Ranzoni					ud
Lemonniera?filiformis R.H. Petersen				d	ud
Lemonniera terrestris Tubaki				ud	ud
Lunulospora curvula Ingold					d
Mycocentrospora acerina (Hartig) Deighton		d			
Mycocentrospora sp. 1 cf. *angulata* R.H. Petersen	d	ud	ud	ud	ud
Mycofalcella calcarata Marvanová				ud	ud
Pleuropedium multiseptatum Marvanová & Iqbal	ud		ud		
Stenocladiella neglecta (Marv. & Descals) Marvanová & Descals		d		ud	u
Taeniospora gracilis Marvanová				ud	ud
Tetrachaetum elegans Ingold	d	ud		ud	ud
Tetracladium furcatum Descals		ud			
Tetracladium marchalianum de Wildeman		ud	ud		
Tetracladium setigerum (Grove) Ingold	u	ud	u		u
Tricellula?aquatica Webster		d	d		
Tricellula?aurantiaca Haskins		ud			
Tricladium attenuatum Iqbal					u
Tricladium?biappendiculatum (Arnold) Marvanová & Descals	d	ud			
Tricladium caudatum Kuzuha					d
Tricladium chaetocladium Ingold				ud	ud
Tricladium curvisporum Descals	d	ud	u		ud
Tricladium patulum Marvanová & Marvan				ud	ud
Tricladium splendens Ingold	ud	ud	ud	ud	ud
Tripospermum camelopardus Ingold. Dann & McDougall	d	u	ud	ud	ud
Tripospermum myrti (Lind.) Hughes				ud	ud
Tripospermum sp. 1 cf.?*prolongatum* Sinclair & Morgan-Jones				d	
Triscelophorus?konajensis Sridhar & Kaveriappa					d
Triscelophorus monosporus Ingold					ud
Varicosporium elodeae Kegel	ud	u	ud	d	u
Varicosporium giganteum Crane				ud	
Ypsilina graminea (Ingold *et al.*) Marvanová & Descals	ud	ud	u		ud