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Effects of whole-stream nutrient enrichment on the concentration and abundance of aquatic hyphomycete conidia in transport

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Abstract: The concentrations and relative abundances of aquatic hyphomycete conidia in water were followed during a three-year study in two headwater streams at Coweeta Hydrologic Laboratory, North Carolina, using the membrane-filtration technique. After a one-year pretreatment period, one of the streams was enriched continuously with inorganic nutrients (N+P) for two years while the other stream served as the reference. This ecosystem-level nutrient manipulation resulted in concentrations of aquatic hyphomycete conidia in the water of the treated stream that were 4.5–6.9 times higher than the concentrations observed during the pretreatment period and in the reference stream. Nutrient enrichment led to an increase in the number of fungal species detected on each sampling date. Changes in dominance patterns and relative abundances of individual species also were detected after treatment. Nutrient addition stimulates the reproductive activity of aquatic hyphomycetes, their colonization success and fungal-mediated leaf-litter decomposition. Such changes in the activity of the fungal community might affect higher trophic levels in lotic ecosystems.

Key words: community structure, freshwater fungi, nitrogen, phosphorus, seasonal pattern

INTRODUCTION

Aquatic hyphomycetes play a key role in the decomposition of plant litter entering woodland streams from riparian vegetation (Suberkropp and Klug 1976, Bärlocher and Kendrick 1981, Bärlocher 1992). These fungi colonize substrata, sporulate underwater, and their conidia are well adapted for dispersal by water currents (Webster and Descals 1981). In laboratory experiments, conidia production may account for 8–12% of leaf mass loss (Suberkropp 1991); lower values (2–4%) have been calculated for fungal communities in streams (Findlay and Arsuffi 1989, Suberkropp 1991).

It was hypothesized that aquatic hyphomycetes might obtain inorganic nutrients (nitrogen and phosphorus) not only from their organic substrata (leaf litter, wood debris, etc.) but also directly from water passing by (Suberkropp 1995, Suberkropp and Chauvet 1995). Later, studies in laboratory microcosms demonstrated that elevated concentrations of nitrate and phosphate in water stimulate overall fungal activity and conidia production (Suberkropp 1998, Sridhar and Bärlocher 2000).

The aim of this study was to examine the effects of long-term, whole-stream nutrient enrichment on the community structure of aquatic hyphomycetes from concentrations of conidia in the water and to compare these data with those from a pretreatment period and a reference stream. Because most aquatic hyphomycetes form characteristic tetraradiate, branched or filiform conidia, the elegant technique introduced by Iqbal and Webster (1973) to characterize aquatic hyphomycete communities in streams was used. It consists basically of passing a known amount of water through membrane filters and subsequently identifying and counting conidia trapped on the filter. The underlying assumption is that assemblages of conidia in transport reflect those developed on submerged organic substrata (Bärlocher 1982); some conidia, however, may be introduced from terrestrial habitats (Bandoni 1981, Sridhar and Bärlocher 1993).

MATERIALS AND METHODS

The study was conducted at two headwater streams draining catchments 53 and 54 at the Coweeta Hydrologic Laboratory, Macon County, North Carolina. They drain south-facing slopes covered by mixed deciduous forest in the southern Appalachian Mountains at an elevation of ca 850 m. Because the dense understory of *Rhododendron maximum* L. results in year-round shading, the streams are primarily heterotrophic, i.e., they rely on allochthonous organic matter and energy. These streams are small (average discharge about 2 L s^{-1}), circumneutral, softwater and contain low nutrient concentrations (NO_3-N + NH_4-N < 29 μg L^{-1}, soluble reactive phosphorus (SRP) < 9 μg L^{-1}, J. Benstead, pers comm). Streams are located about 300 m apart, and their physical and hydrochemical characteristics are very

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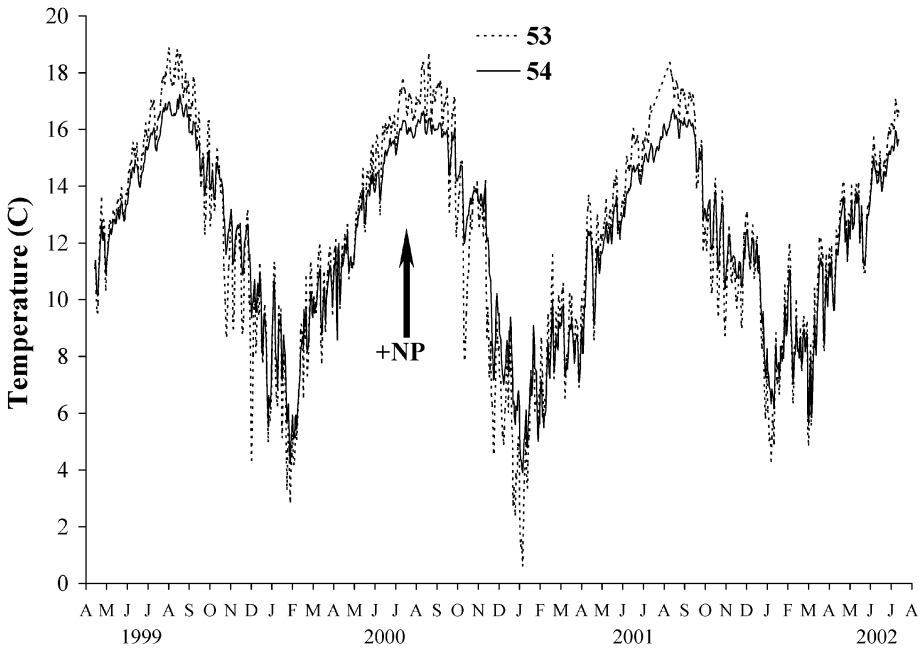

FIG. 1. Average daily water temperatures of stream 53 and 54 during the study.

similar (Cuffney et al 1990, Wallace et al 1999). Water temperature during the study was continuously monitored with Optic StowAway temperature probes (Onset Computer Corp.).

Pretreatment observations of both streams were initiated in Apr 1999, and nutrient addition was started in stream 54 on 11 Jul 2000, while stream 53 continued to serve as a reference. Treatment stream 54 was enriched with nitrogen and phosphorus (ammonium nitrate and potassium phosphate) with a pump 145 m above the sampling site that added a concentrated solution into a pipe fed with stream water that was laid in the streambed and continued to within 10 m of the downstream flume. The amount of nutrients added was proportional to instantaneous discharge and was controlled by a data logger. The pipe had 18 openings (an average of 8 m apart) down the stream, letting nutrient solution drip into the stream over its entire length (Gulis and Suberkropp 2003a). Nutrient addition resulted in elevated ammonium-N (100 μg L^{-1}, mean during 24 mo of treatment), nitrate-N (283 μg L^{-1}) and SRP (46 μg L^{-1}) that was determined from five water samples taken at approximately 25 m intervals along the stream twice a month (J. Benstead, pers comm).

To determine concentrations and species composition of aquatic hyphomycete conidia, water samples were taken monthly over a 3 yr period (Apr 1999–Jul 2002) at flumes 135 and 190 m downstream from the source of streams 53 and 54, respectively. Triplicate samples of stream water (300–500 mL) were filtered through membrane filters (5 μm pore size, Millipore) at streamside (Iqbal and Webster 1973), and conidia were stained with trypan blue in lactic acid (0.1%). Filters were taken to the laboratory where conidia were identified and counted (150 fields, Leitz Laborlux, 160×). Different amounts of water were filtered and subjected to counts of conidia on each date, due to the highly variable concentrations of suspended solids that interfered with conidia observation and according to anticipated conidia concentrations. To meaningfully compare species richness, we adjusted all conidia counts to the smallest sample volume (3 × 300 mL) and used rarefaction (Krebs 1989) to calculate the expected number of species corresponding to the adjusted number of conidia in each sample. In other words, we chose to use the volume of water sampled and not the number of conidia (individuals) to standardize species richness (see Bärlocher and Graça 2002 for discussion).

Mean aquatic hyphomycete conidia concentrations and numbers of species in the water of stream 53 and 54 were compared both before and after treatment periods with paired *t*-tests. Conidia concentrations were $\log_{10}$ transformed before analyses. To find out whether treatment indeed caused the changes in conidia concentrations, we performed randomized intervention analysis (RIA, Carpenter et al 1989). Despite recent criticism (Murtaugh 2002), we believe that this analysis was appropriate in our case because the three half-series means (mean pretreatment conidia concentrations in both streams and mean post-treatment concentration in the reference stream) were very similar and temporal differences between streams were not clearly pronounced. Sorensen's quantitative similarity indexes (Magurran 1988) were calculated as:

$$SI = 2\frac{\sum_{k=1}^{S} \min(x_{ik}, x_{jk})}{\sum_{k=1}^{S} \min(x_{ik} + x_{jk})}$$

where S is the number of species, x_{ik} is the relative abundance of species k in stream i. Evenness of conidia distribution among taxa and Shannon-Wiener diversity index were calculated as:

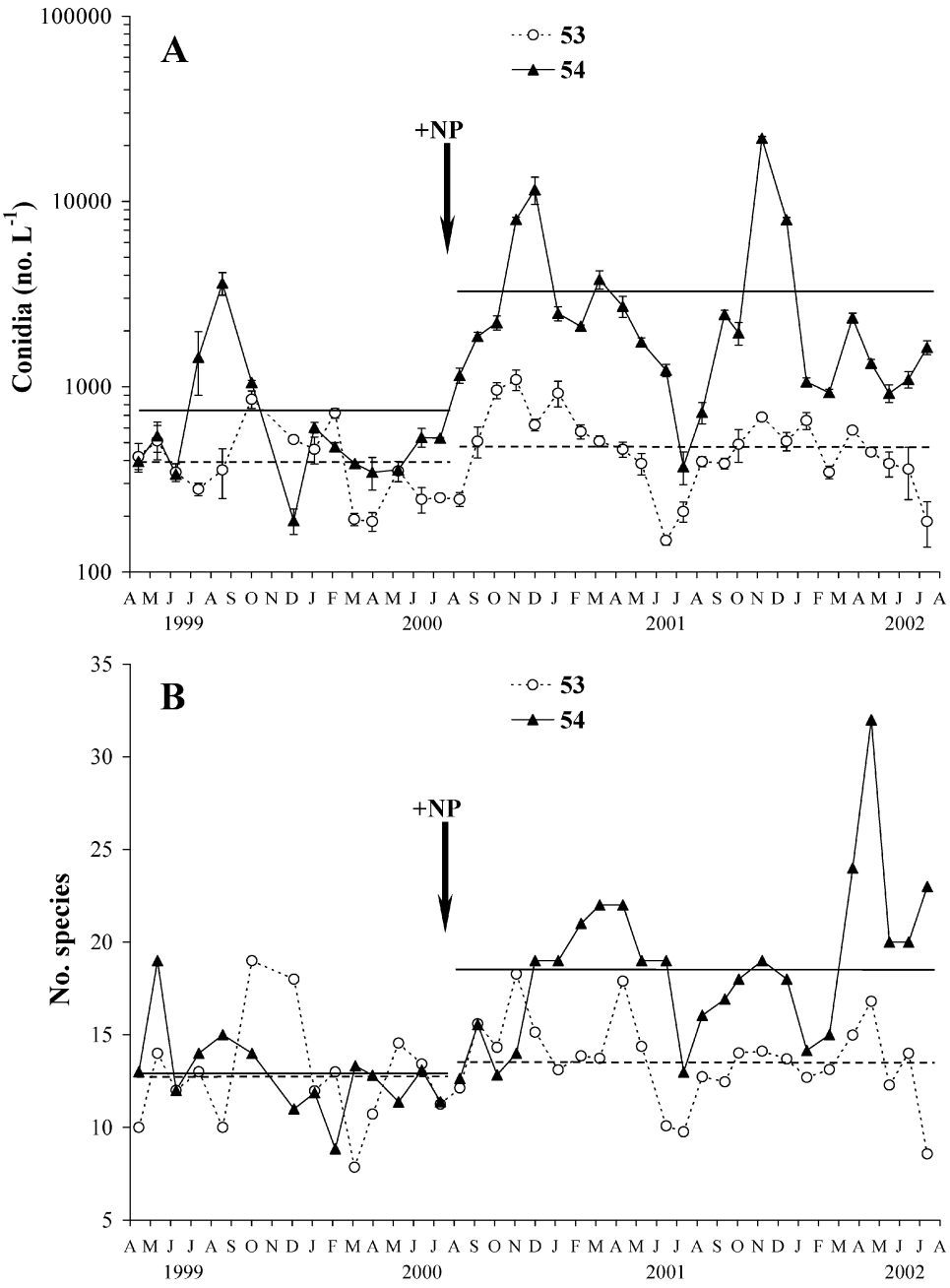

FIG. 2. Conidia concentration (A) and species richness (B) of aquatic hyphomycetes in water of stream 53 and 54. Symbols indicate mean ± 1 SE. Means for stream 53 (dashed) and 54 (solid lines) are presented for before and after treatment periods.

$$E = \frac{H}{H_{\max}} = \frac{-\sum_{i=1}^{S} p_i \ln p_i}{\ln S}$$

where E is evenness, H is Shannon-Weaver index, S is the number of species, p_i is the relative abundance of species i in the community. Cluster and correspondence analyses based on mean relative abundances of dominant fungal species (abundance >5% in any stream/treatment combination, nine species total) were carried out to ordinate four stream/treatment combinations and analyze what changes in fungal species/abundances led to the differences observed. Statistical analyses were done with Statistica 5.5 (StatSoft Inc., Tulsa, Oklahoma).

RESULTS

Water temperatures were very similar in the two streams throughout the study (FIG. 1). Although the concentration of aquatic hyphomycete conidia in stream water from 53 and 54 fluctuated rather errat-

TABLE I. Aquatic hyphomycete conidia assemblages (mean of percent contributions at each sampling date) in water from stream 53 (reference) and 54 (treatment) before (Apr 1999–Jul 2000) and during (Jul 2000–Jul 2002) the addition of nutrients to stream 54

Aquatic hyphomycete	Stream/period			
	53 before	54 before	53 after	54 after
**Alatospora acuminata* Ingold aggreg.	14.7	6.8	14.5	3.1
Alatospora pulchella Marvanová		0.03		0.5
Anguillospora crassa Ingold			0.05	
**Anguillospora filiformis* Greath.	6.1	11.9	4.5	16.3
Anguillospora cf. *furtiva* J. Webster & Descals	0.5	0.1	0.2	0.6
Anguillospora cf. *rosea* J. Webster & Descals	0.03	0.04	0.1	0.04
**Articulospora tetracladia* Ingold	17.3	14.4	16.5	9.3
Casaresia sphagnorum Gonz. Frag.	4.5	1.1	4.9	1.4
Clavariopsis aquatica De Wild.	0.2	0.2	0.2	0.5
Clavatospora longibrachiata (Ingold) Marvanová & Sv. Nilsson	0.04	0.05	0.1	0.1
Culicidospora aquatica R.H. Petersen	0.04	0.1	0.1	0.2
Dactylella microaquatica Tubaki	0.05	0.02	0.1	0.1
Dendrospora erecta Ingold	0.1	0.1	0.1	0.2
Dimorphospora foliicola Tubaki	+	+	+	+
Dwayaangam cf. *dichotoma* Nawawi	0.1			
?*Dwayaangam* sp.	0.2	0.1		
**Flagellospora curvula* Ingold	3.6	0.8	5.4	5.2
Fontanospora alternibrachiata Dyko	1.0	0.1	2.0	0.04
Fontanospora eccentrica (R.H. Petersen) Dyko	0.02	0.01	0.02	0.01
Goniopila monticola (Dyko) Marvanová & Descals		0.1		0.3
Heliscella stellata (Ingold & V.J. Cox) Marvanová	0.2	0.3	0.5	0.3
Heliscina antennata Marvanová	0.1	0.02	0.1	0.1
Heliscina campanulata Marvanová	0.3	0.3	0.6	0.6
Heliscus lugdunensis Sacc. & Thérry	0.8	0.8	1.0	0.8
Isthmotricladia britannica Descals		0.04		
Lateriramulosa uniinflata Matsush.	0.9	0.3	0.9	0.3
Lemonniera aquatica De Wild.	0.2	0.01	0.1	0.01
Lemonniera pseudofloscula Dyko	1.2	0.5	1.0	0.2
Lemonniera terrestris Tubaki	0.2		0.2	
**Lunulospora curvula* Ingold	0.3	7.6	0.04	3.9
Mycofalcella calcarata Marvanová et al.	0.2	0.5	0.2	1.6
Pleuropedium tricladioides Marvanová & S.H. Iqbal	0.04		0.2	
Stenocladiella neglecta (Marvanová & Descals) Marvanová & Descals			0.05	0.1
Taeniospora gracilis var. *enecta* Marvanová & Stalpers	4.9	2.3	3.6	3.5
**Tetrachaetum elegans* Ingold	5.3	7.2	5.7	12.2
Tricladium biappendiculatum (G.R.W. Arnold) Marvanová & Descals		0.01		0.04
**Tricladium chaetocladium* Ingold	1.5	3.9	1.5	11.3
Tricladium sp.		0.1		
Trinacrium sp.	0.3	0.4	0.2	0.2
Tripospermum myrti (Lind) S. Hughes	0.5	0.1	0.3	0.1
Tripospermum cf. *prolongatum* R.C. Sinclair & Morgan-Jones	0.3		0.3	0.03
Tripospermum sp.	0.3	0.1	0.3	0.03
**Triscelophorus konajensis* K.R. Sridhar & Kaver.	6.1	6.3	3.0	3.2
**Triscelophorus monosporus* Ingold	5.1	8.6	5.2	4.0
Variocladium giganteum (S.H. Igbal) Descals & Marvanová	0.2		0.5	
*Sigmoid conidia (<60 μm long)	12.4	16.6	15.5	13.4
Sigmoid conidia (60–120 μm long)	2.8	3.5	2.7	1.7
Sigmoid conidia (>120 μm long)	3.7	2.5	3.1	2.2
Unidentified conidia #1 (H-shaped)	0.2	0.1	0.2	0.2
Unidentified conidia #2 (pentaradial)	1.3	0.5	0.5	0.1
Unidentified tetraradiate conidia	1.9	1.6	3.7	2.0
Number of species	44	44	44	43

ically during the pretreatment period in 1999–2000, mean conidia concentrations in the two streams were not significantly different (paired *t*-test, $P = 0.084$, FIG. 2A). In 2000–2002, when nutrients were continuously added to stream 54, the difference in mean conidia concentration between reference and treatment streams was highly significant ($P < 0.0001$, FIG. 2A). On the basis of the comparison of pretreatment and treatment data for both streams, RIA indicated that the treatment had an effect on conidia concentrations in the water ($P < 0.0001$). Nutrient enrichment resulted in higher conidia concentrations on each sampling date in stream 54 in comparison to 53. Seasonal patterns with higher conidia concentrations in the autumn and early winter also was more pronounced in the treatment stream.

A total of 51 taxa of aquatic and water-borne hyphomycetes were detected in the two streams during the study (TABLE I). The mean numbers of species per sampling date (sample volume adjusted, rarefied data) were nearly equal and not significantly different in stream 53 and 54 during the pretreatment period (paired *t*-test, $P = 0.896$, FIG. 2B, TABLE II). However, the mean number of species per sampling date was higher in stream 54 compared to stream 53 during the treatment period (paired *t*-test, $P < 0.0001$). Species richness of aquatic hyphomycetes determined from water samples was affected positively by nutrient enrichment in stream 54 (RIA, $P = 0.002$). Temporal fluctuations in species richness were similar in both streams during the treatment period and generally corresponded to seasonal patterns in conidia concentration (cf. FIG. 2A AND B).

Five and seven species of aquatic hyphomycetes dominated the conidia pool (mean percent contribution >5% during study period) in stream 53 and 54, respectively. The relative abundances of the dominant species are illustrated in FIG. 3. The top-ranked species in both streams was *Alatospora acuminata* (28 and 18% of total conidia in stream 53 and 54, respectively, but see note to TABLE I for explanation). The most notable difference in community structure of aquatic hyphomycete conidia between streams throughout the observation period was the nearly total absence of *Lunulospora curvula* from stream 53, whereas in 54 it was a codominant species at least in the pretreatment year (TABLE I, FIG. 3). Nutrient enrichment resulted in shifts in relative abundances of some aquatic hyphomycetes in stream 54. *Triscelophorus monosporus* and *L. curvula* were common during the pretreatment period in warmer seasons and in the summer (2000) when the enrichment was started but nearly disappeared afterward. In contrast, *Tricladium chaetocladium* and *Tetrachaetum elegans* increased their contribution to the total conidia pool after nutrient addition started (TABLE I, FIG. 3).

Despite the fact that we observed changes in dominant species and the relative contributions of individual fungal species to the total conidia pool, species richness, diversity and evenness of conidia distribution among taxa were similar in all four stream/treatment combinations (TABLE II). The similarity indices between fungal assemblages, however, indicate that changes in aquatic hyphomycete community structure occurred after nutrient enrichment.

Cluster and correspondence analyses also reflected changes in aquatic hyphomycete communities that took place after nutrient enrichment and allowed separation of the ''54 after'' fungal assemblage (FIG. 4). Increases in relative abundances of the conidia of *Anguillospora filiformis*, *Tetrachaetum elegans* and *Tricladium chaetocladium* were associated with nutrient addition (TABLE I, FIG. 4). Overall, 70.0 and 27.3% of the inertia were explained by dimension 1 and 2, respectively, of the correspondence analysis.

DISCUSSION

In our study, we achieved 13- and fivefold mean increases in nitrogen and phosphorus concentrations in the treatment stream that led to 4.5–6.9 times higher mean conidia concentrations during the treatment period in comparison to pretreatment period and the reference stream (FIG. 2A, TABLE II). The maximum conidia concentration recorded in stream 54 was 22 000 spores L^{-1}, which is similar to some of the higher concentrations reported for other streams (cf. 22 000 spores L^{-1}, Shearer and Webster 1985a; 25 000 spores L^{-1}, Suberkropp 1991; 18 000 spores L^{-1}, Suberkropp 1997; 24 000 spores L^{-1}, Gönczöl and Révay 1998).

In addition to nutrient concentrations, two important factors that affect production of conidia are temperature (cf. FIGS. 1 and 2A) and presence of leaf

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* Indicate dominant species used in cluster and correspondence analyses. Data for *Alatospora acuminata* conidia and sigmoid conidia <60 μm were combined since numerous isolates obtained from these sigmoid conidia later appeared to be *A. acuminata sensu stricto*; however, species with truly filiform conidia might have been present but could not be positively identified on the basis of detached conidia.

+ Not counted because of similarity to propagules of other organisms (ellipsoid conidia).

TABLE II. Comparison of aquatic hyphomycete communities of stream 53 (reference) and 54 (treatment) before and after nutrient addition was started in 54. Standard errors are included for mean conidia concentrations and number of species

Parameter	53 before (n = 14)	54 before (n = 14)	53 after (n = 24)	54 after (n = 24)
Mean conidia concentration (L^{-1})	407 ± 52	772 ± 236	503 ± 48	3481 ± 971
Mean number of species per date	12.8 ± 0.8	12.9 ± 0.6	13.7 ± 0.5	18.5 ± 0.9
Total number of species	44	44	44	43
Shannon-Wiener index*	1.82	1.96	1.84	1.89
Evenness*	0.48	0.52	0.49	0.50
	53 before–54 before	53 before–53 after	54 before–54 after	53 after–54 after
Similarity index*	0.73	0.90	0.73	0.65

* Calculated from mean conidia abundances.

litter in the stream. Headwater streams at Coweeta have relatively high leaf-litter standing stocks throughout the year (Suberkropp, unpubl data). This, coupled with naturally very low N and P concentrations and relatively warm winter temperatures, results in small fluctuations in conidia concentrations throughout the year (stream 53, FIG. 2A, cf. Suberkropp and Wallace 1992) rather than large peaks during the autumn-winter that are common in many temperate streams (Iqbal and Webster 1973, Bärlocher and Rosset 1981, Shearer and Webster 1985b, Suberkropp 1997, Gönczöl and Révay 1999, Bärlocher 2000). Nutrient enrichment of stream 54, however, led to clear seasonal peaks coinciding with or lagging slightly behind the main leaf-litter inputs in autumn (stream 54 Nov 2000 and 2001, FIG. 2A). Smaller peaks were also observed in spring.

Several studies have provided indications that water chemistry and inorganic nutrients in particular, affect conidia production to a greater extent than fungal biomass accrual and microbially mediated leaf-litter decomposition (Suberkropp 1995, Suberkropp and Chauvet 1995, Grattan and Suberkropp 2001). These observations also were confirmed by experiments in laboratory microcosms (Suberkropp 1998, Sridhar and Bärlocher 2000). Increased concentrations of conidia in streams with high nutrient concentrations should result in more efficient/faster colonization of new substrata. Once established on plant litter, fungi grow faster with higher nutrient availability (Grattan and Suberkropp 2001, Gulis and Suberkropp 2003a) and because of their relatively short lifecycle soon produce more conidia. This stimulation of fungal activity leads to the faster disappearance of leaf litter from the stream, which might affect leaf-shredding invertebrates and stream food webs.

Aquatic hyphomycetes allocate up to 80% of their production to conidia (Suberkropp 1991), and the proportion can vary depending on nutrient availability (Suberkropp 1995). Because fungal yield coefficients for decomposing submerged leaf litter were estimated to vary between 1–31%, being higher (15–31%) at increased nutrient availability (Suberkropp 1991, 1995, Weyers and Suberkropp 1996, Sridhar and Bärlocher 2000, Gulis and Suberkropp 2003b, c), this results in a significant amount of leaf carbon being lost as conidia. In laboratory microcosms, *Articulospora tetracladia* converted 1.5 and 12% of leaf mass loss to conidia at low and high nutrient concentrations, respectively (Gulis and Suberkropp 2003c). For leaf litter colonized by a natural microbial assemblage in a headwater stream and then incubated in laboratory microcosms at different levels of nutrients, the difference was even greater—0.04 and 4.0% of leaf mass loss was converted to conidia at low and high N and P concentrations, respectively (Gulis and Suberkropp 2003b). Consequently, in streams with higher nutrient concentrations, more conidia, i.e., more fine-particulate organic carbon, will be produced with the potential to be transported out of a stream and lost to local food webs.

Species richness of aquatic hyphomycetes in stream 54 after nutrient addition was higher than in the reference stream on each sampling date after late fall 2000 (FIG. 2B). This presumably was due to uneven increase in sporulation by aquatic hyphomycetes that enhanced the detection of rare species. We also noticed shifts in the relative contributions of the dominant species (FIG. 3). In contrast, Sridhar and Bärlocher (2000) did not find shifts in species composition in response to nutrient addition in a laboratory experiment. It is not clear why elevated nutrient concentrations affected the relative abundances of some dominant species. We noted that all three species that significantly increased in abundance after nutrient addition (*Anguillospora filiformis*, *Tetrachaetum elegans* and *Tricladium chaetocladium*; TABLE I, FIG. 4) have relatively large conidia in comparison to spore size of species dominant during pretreatment period or in the reference stream (*Alatospora acuminata* and *Articulospora tetracladia*). Perhaps production of co-

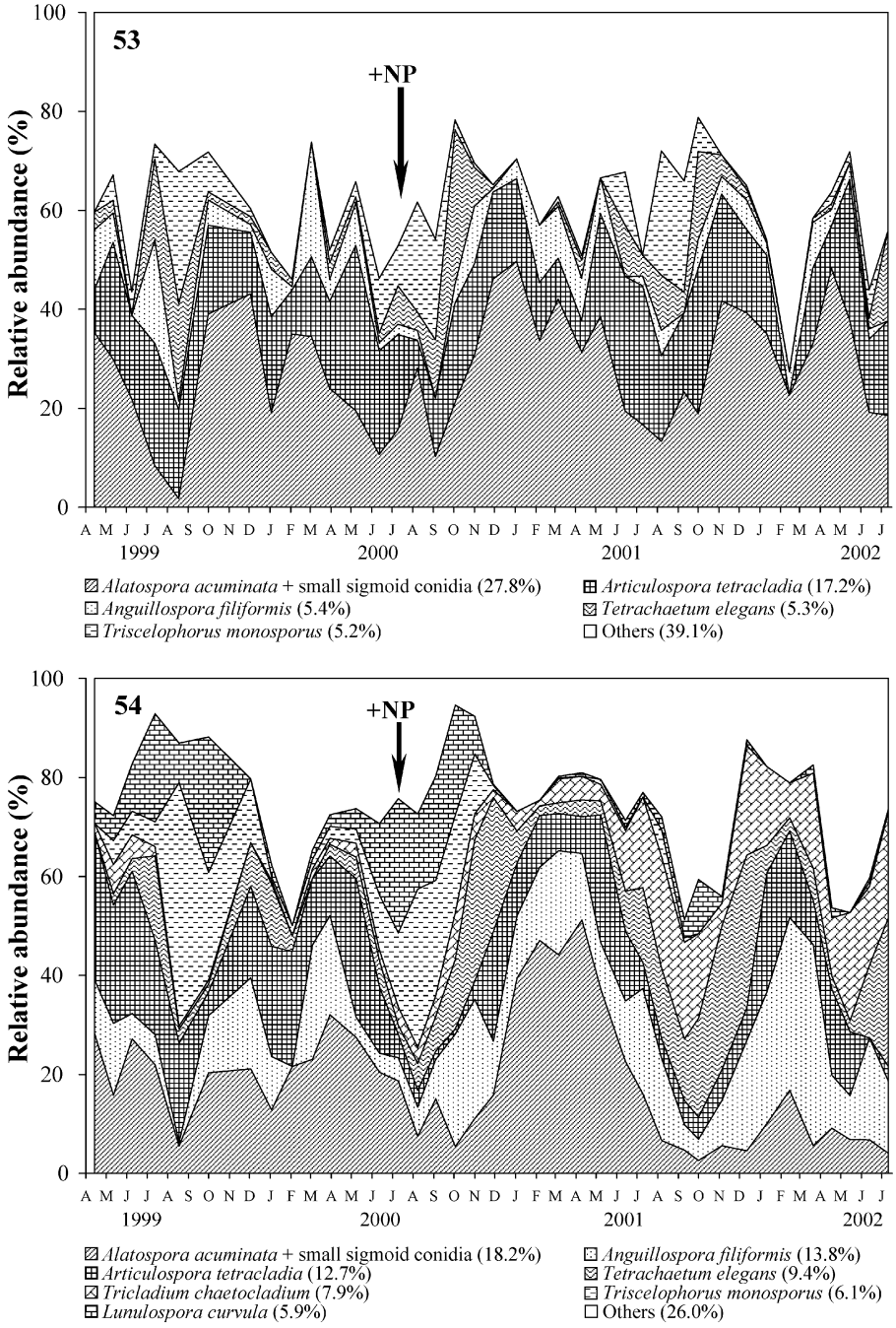

FIG. 3. Relative abundance of dominant aquatic hyphomycetes (as conidia in transport) in streams 53 and 54 throughout the study. Data for *Alatospora acuminata* and small sigmoid conidia were combined (see note to TABLE I).

nidia with higher biovolume requires additional inorganic nutrient supply because it has been suggested that N and P obtained from the water are mainly shunted to sporulation by aquatic hyphomycetes (Suberkropp 1998). Additional studies on the physiological requirements of particular species are needed to address this question. Interspecific interactions also may be modified at different nutrient levels.

The effects of long-term, whole-stream, nutrient enrichment on aquatic fungi has received little attention in the literature. We previously compared fungal biomass, leaf-litter decomposition and aquatic hyphomycete conidia in transport in the upstream, unenriched reach of stream 54 with that occurring in the nutrient-enriched downstream reach in a shorter (8 mo) study (Gulis and Suberkropp 2003a). Concen-

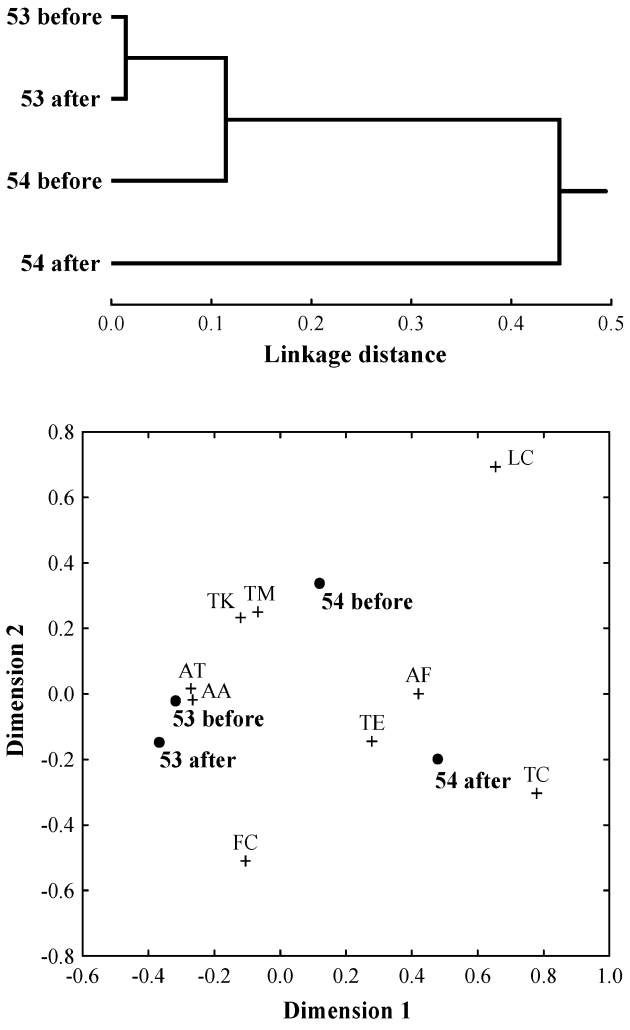

FIG. 4. Cluster and correspondence analyses of four stream/treatment combinations based on mean relative abundances of conidia of nine dominant species of aquatic hyphomycetes. Clustering based on Pearson correlation coefficient and unweighted pair-group average method. Solid circles on correspondence analysis plot represent communities, crosses plot fungal taxa are abbreviated as: AA = *Alatospora acuminata*, AF = *Anguillospora filiformis*, AT = *Articulospora tetracladia*, FC = *Flagellospora curvula*, LC = *Lunulospora curvula*, TE = *Tetrachaetum elegans*, TC = *Tricladium chaetocladium*, TK = *Triscelophorus konajensis*, TM = *T. monosporus*.

trations of conidia were higher in the downstream reach, and some shifts in dominance pattern similar to those observed in our study occurred. It is evident from the results of these studies that nutrient enrichment of a small woodland stream (including anthropogenic eutrophication) can result in higher concentrations of aquatic hyphomycete conidia in transport and changes in fungal community structure. Because these changes are coupled to faster leaf-litter colonization, higher decomposition rates (Gulis and Suberkropp 2003a) and presumably increased transport of fine particulate organic matter downstream, such enrichment might have consequences for the invertebrate fauna feeding on submerged decaying organic matter and on the higher trophic levels in such streams.

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