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Fungal communities and biomass in mountain streams affected by mine drainage

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With 6 figures and 3 tables

Abstract: We examined fungi associated with decomposing leaves in streams to understand the effects of mine drainage on this community and to test a general model of ecological response to stress. The community composition and biomass of fungi and microbial activity associated with decomposing willow leaves were determined for 20 Colorado mountain stream sites, some of which were affected by mine drainage. The pH, concentration of dissolved zinc, and deposition rate of metal oxides were measured at each site. The community composition of fungi on willow leaves from litterbags was determined by analysis of conidia from aerated leaves and a particle-plating method. As with other communities in streams, diversity of fungal communities was sensitive to low pH and high concentrations of zinc from mine drainage, whereas biomass and functioning were stable under stress from pH or zinc. Diversity was low at sites with high concentrations of dissolved zinc (>1 mg/L) or low pH (<6). Fungal biomass (concentration of ergosterol) and microbial activity, in contrast, often were high despite the chemical conditions of the streams and the limited diversity of fungi. Microbial respiration was negatively related to the physical stress of metal oxide deposition. The concentration of ergosterol was significantly related to rates of respiration on leaves at pristine sites. Leaves from sites with high concentrations of dissolved zinc often had higher fungal biomass and microbial respiration than leaves from pristine sites. Several sites of low pH had high rates of respiration on leaves and visible fungal growth, but little or no measurable ergosterol. Leaves at these sites had ergosterol-like compounds that have yet to be identified.

Key words: fungi, hyphomycetes, ergosterol, mine drainage, metals, litter breakdown, streams.

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Introduction

The effects of stress on freshwater ecosystems have been studied intensively over the last several decades. Based on the general predictions of ODUM (1985) and previous studies (SCHINDLER 1987, HOWARTH 1991), NIYOGI et al. (in press) presented a conceptual model of ecosystem response to a gradient of stress. The model predicts that biodiversity will be sensitive to low levels of stress, whereas compensation by tolerant taxa for the loss of sensitive taxa will allow stable biomass and functioning until very high levels of stress. We tested this model by examining fungal communities from decomposing leaves in mountain streams affected by stressors from mine drainage.

Aquatic fungi play a major role in the breakdown of litter in streams (SUBERKROPP 1998). Several recent studies suggest that fungi, especially aquatic hyphomycetes, are the dominant microbial decomposers of litter during the early stages of breakdown (BALDY et al. 1995, SUBERKROPP & WEYERS 1996). Fungi not only mineralize litter, but also make litter more palatable and nutritious to invertebrate consumers (shredders) (BÄRLOCHER 1985, SUBERKROPP 1992).

Fungal abundance and activity on litter in pristine streams are affected by several factors. The quality of litter affects the composition, biomass, and activity of fungal communities (SUBERKROPP 1998). Additionally, fungal activity usually is greater at higher temperature and with greater concentrations of dissolved nitrogen and phosphorus (SUBERKROPP 1995, SUBERKROPP & CHAUVET 1995, GRATTAN & SUBERKROPP 2001). Finally, while fungi affect the feeding preference and nutrition of shredders, shredders may also affect fungi through competition for litter or direct consumption of fungi (SUBERKROPP 1992).

Fungal communities and their breakdown of litter in streams can be affected by anthropogenic stress (BÄRLOCHER 1992, CHAMIER 1992, MALTBY 1992, BERMINGHAM 1996), including the effects of mine drainage (MALTBY & BOOTH 1991, BERMINGHAM et al. 1996, KRAUSS et al. 2001). Mine drainage, however, can impose several distinct stressors on stream biota through its acidity, high concentrations of dissolved metals, and metal oxide deposition (MCKNIGHT & FEDER 1984, KELLY 1988), all of which can have different effects on stream biota and ecological processes (NIYOGI et al. 1999, 2001).

NIYOGI et al. (2001) measured litter breakdown in streams affected by mine drainage and examined the contributions of invertebrates and microbes to rates of litter breakdown. They found that microbial activity on willow leaves was affected negatively by deposition of metal oxides, but not by elevated concentrations of zinc or acidity from mine drainage. We report here results from a companion study that examined fungal communities, biomass, and microbial activity over time on decomposing leaves in 20 mountain streams, 13 of which

were affected by mine drainage. We expected the response of fungal communities to be similar to that of algal communities in these streams. NIYOGI et al. (in press) found that algal diversity was low in streams with low pH or high concentration of dissolved metals, whereas biomass and primary production were high at even the most stressed sites. The deposition of metal oxides did, however, affect both algal biomass and primary production. Here, we hypothesized that fungal diversity would also be sensitive to the chemical stresses of low pH and dissolved metals. Fungal biomass and activity, conversely, were predicted to be stable under chemical stress but to decline under the physical stress of metal oxide deposition.

Methods

Site descriptions

All study sites were situated on low-order streams at high elevation (2700–3400 m a.s.l.) in the Rocky Mountains of Colorado, USA. Riparian vegetation consisted mostly of willows (*Salix* spp.), but included some aspen (*Populus tremuloides*), pine (*Pinus* spp.), and spruce (*Picea* spp.). Seven sites had no visible inflows of mine drainage and showed no chemical indication of mine drainage; these sites were considered pristine with respect to effects of mine drainage. Thirteen other sites were affected to varying degrees by mine drainage. Further descriptions of the study sites can be found in NIYOGI et al. (2001).

Abiotic characteristics of streams

pH was measured in the field with an ion-specific electrode. Concentrations of metals in filtered (Whatman GF/F, nominal pore size 0.7 μm) streamwater were measured by ICP-AES or AA spectroscopy. Zinc was the main dissolved metal of ecological concern at our sites (NIYOGI et al. 2001) and the only one included in the present data analysis. The deposition rate of metal oxides onto the streambed was quantified as the accumulation of ash mass on cobbles over time. Cobbles were randomly selected from the stream, brushed clean of deposits, and returned to the stream in areas of moderate surface velocity (10–30 cm/s). After 4–12 weeks, deposits that had accumulated on the cobbles were brushed into a weighing dish for determination of ash mass. Deposits from some sites were digested and analyzed for metals (AA spectroscopy) to confirm that the deposits were indeed iron and aluminum oxides. The upper surface area of the cobbles was determined by a foil wrap method (STEINMAN & LAMBERTI 1996). Deposition rates were calculated as the average ash mass per unit area of surface area per unit time for 3–10 replicates. Our measures of abiotic characteristics are the same as those used in data analysis in NIYOGI et al. (2001), which focused on rates of litter breakdown.

Litterbags

Fungal communities were examined on leaves held in litterbags placed in streams (NIYOGI et al. 2001). Litterbags consisted of plastic tubes (diameter = 5 cm) that had 1 mm nylon mesh covering both ends, although the upstream end had holes poked in the mesh to allow access to invertebrates. Each litterbag contained 1 g dry mass of willow leaves (*Salix* sp.) that had been collected just prior to abscission the previous autumn and air-dried. Litterbags were placed in 20 sites at the start of autumnal leaf fall in the area (near the end of September). Litterbags were collected over the course of 3–4 months (3 replicate litterbags at each sampling), and the fungal communities on the remaining leaves were examined. Sampling occasions varied from 4 to 8 across the sites.

Fungal communities

Fungal community composition was described by two methods. First, production of conidia by aquatic hyphomycetes was examined as described by SUBERKROPP (1995). Five discs (1-cm diameter) of leaf material taken from litterbags were placed in sterile tubes containing filtered stream water. Discs were taken from along sides of leaves, avoiding the midrib. The water and leaf discs were acrated for about 48 hours at 10 °C. Water from the tubes was filtered (5 µm pore size), and the filters were stained with trypan blue (0.1 % in lactic acid) and examined at 100× to 400× under a compound microscope. Conidia were identified following INGOLD (1975) and WEBSTER & DESCALS (1981) and counted.

The second method for analysis of fungal community composition involved a particle plating method (KIRBY et al. 1990). The same discs that were used for analysis of conidia were broken into small particles with a blender. Leaf particles between 100 and 400 µm were plated onto a weak malt extract agar (0.25 %) containing antibiotics (24 µg ai/mL streptomycin, 300 i.u./mL penicillin – KIRBY et al. 1990) to inhibit bacteria. Plates were incubated at 10 °C for several days and then checked for development of colonies. Strips of agar with fungi were aerated and sampled as outlined above for production of conidia. Fungi other than aquatic hyphomycetes that developed in the agar were examined based on morphology or spore type, and classified as distinct but unknown taxa (i.e., unknown #1, unknown #2, etc.) for estimation of diversity.

Our taxonomic analysis was fairly coarse compared to other studies, but it provided data with which we could calculate indices of diversity. The Shannon-Wiener diversity index (HUTCHINSON 1967) was calculated from counts of conidia or cultured colonies. Community composition data from fungi on leaves that had been in the stream for 21–80 days were pooled for the calculation of diversity indices at each site.

Fungal biomass was estimated by ergosterol extraction and quantification (NEWELL 1993). Ergosterol analysis was conducted on leaves from each site at each sampling, which varied from 4–8 depending on the site. Discs taken from leaves in litterbags were extracted in methanol (HPLC grade) by refluxing for 2 hours. Ethanolic KOH was added, and heating continued for a further 30 minutes. Ergosterol was partitioned into pentane (HPLC grade), evaporated to dryness under N_2, and redissolved in 1 mL of methanol. Extracts were sonicated for 5 minutes, filtered (0.45 µm PTFE fil-

ter), and analyzed by HPLC for ergosterol (NEWELL 1993). A 100-µL sample was separated on a C-18 column at a flow rate of 1.0 mL/min with HPLC-grade methanol as the mobile phase. Ergosterol eluted at about 10 min and was detected by absorbance at 282 nm. Standards of pure (98 %) ergosterol and spiked samples were run each day. As mentioned in the results and discussion, HPLC chromatograms from leaves incubated at very acidic sites often had large peaks that eluted either before (at about 9 min) or after (13 min) ergosterol. These unidentified compounds had UV spectra that were similar to ergosterol (peak absorbance at 282 nm), indicating that they may be ergosterol-like compounds (see Discussion).

The respiration rate of decomposing leaves was used as a measure of microbial activity at each sampling (4–8 times per site) as described by NIYOGI et al. (2001). Three discs of 1-cm diameter were enclosed in a 26-mL vial that contained filtered stream water. Vials were incubated at 10 °C for 18 to 24 hours. Each vial was gently stirred during the incubation. Preliminary trials indicated that oxygen consumption was linear over the period of incubation. Oxygen consumption (respiration) was determined from changes in dissolved oxygen, correcting for controls that had only streamwater. We report microbial respiration as micrograms of O_2 consumed per milligram AFDM of leaf material per hour. NIYOGI et al. (2001) reported rates of microbial respiration from the same assays, but calculated average respiration rates per area of leaves for each site.

Statistical analyses

Statistics were performed with SAS software (Release 8.00). Certain data (zinc concentration, metal oxide deposition) were log-transformed to improve consistency with assumptions of parametric statistics. Simple and multiple (stepwise) linear regression procedures were used to examine relationships between stressors from mine drainage and fungal responses.

Results

Conidia were produced on aerated cores of leaves at all pristine sites, and at most sites affected by mine drainage that had circumneutral pH. Common taxa of fungi are listed in Table 1. *Lemonniera aquatica* was the most common species of aquatic hyphomycete at most pristine sites. Other common taxa at pristine sites included *Clavariopsis aquatica* and *Anguillospora longissima.*

Conidia were not produced from aerated leaves at acidic sites (pH < 5) or sites with very high concentrations of zinc (> 5 mg/L). Particle plating showed that some aquatic hyphomycetes, such as *Varicosporium elodea* and an unidentified species with sigmoid conidia, were common at stressed sites, even though they did not produce conidia during aeration of leaves. Fungal taxa at sites with the lowest pH (< 3) and highest zinc (> 20 mg/L) did not produce conidia upon aeration of the leaves or agar strips from cultures.

Table 1. Common taxa of fungi present at four classes of sites in streams with varying effects of mine drainage in Rocky Mountains of Colorado, USA. Site description refers to the main stressor(s) from mine drainage that affect the sites.

Site description	Number of sites	Common taxa
Pristine	7	*Lemonniera aquatica, Clavariopsis aquatica, Tetracladium marchalianum, Flabellospora* sp., *Anguillospora longissima, Alatospora* sp.
High concentrations of zinc	4	*Lemonniera aquatica,* Unidentified (septate hyphae, no conidia)
pH <3	2	Unidentified (septate hyphae, no conidia)
pH <6 and metal oxide deposition	7	*Varicosporium elodeae,* Unidentified (sigmoid conidia)

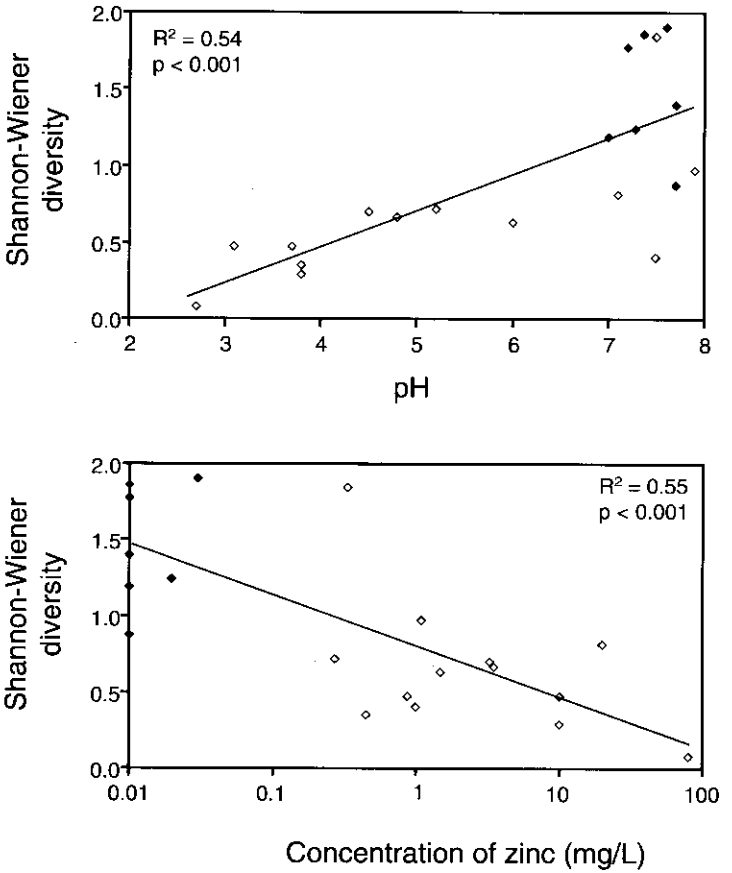

Fig. 1. Diversity (Shannon-Wiener index) of fungal communities on litter versus pH and zinc concentration. Closed diamonds represent sites that were considered pristine; open diamonds represent sites affected by mine drainage.

Table 2. Multiple regression analysis of fungal diversity on litter in relation to stressors from mine drainage.

Dependent variable	Degrees of freedom	Overall R^2	Overall p value	Independent variable	Standardized regression coefficient	p value
Diversity	2, 17	0.66	0.0001	pH	+0.41	0.03
				Zn	−0.43	0.03

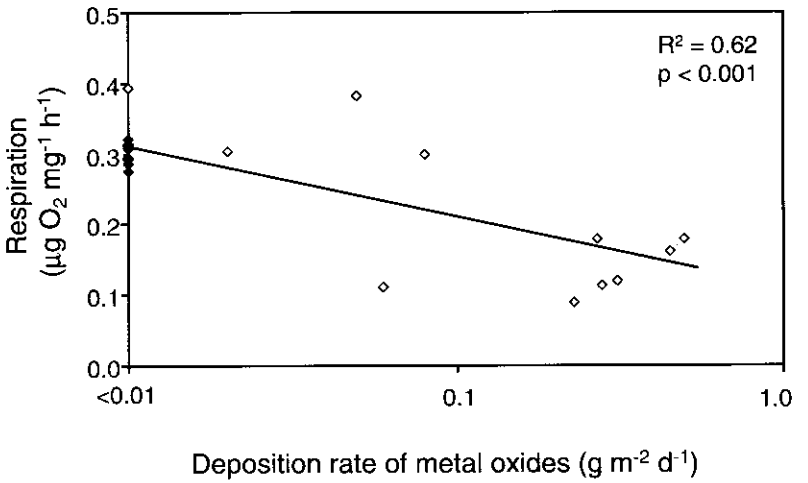

Fig. 2. Rate of respiration versus deposition rate of metal oxides. Closed diamonds represent sites that were considered pristine; open diamonds represent sites affected by mine drainage.

Diversity of fungi was significantly ($p<0.01$) higher at pristine sites (mean diversity = 1.46, S.E. = 0.15, n = 7) than at sites affected by mine drainage (mean diversity = 0.65, S.E. = 0.12, n = 13 sites). Diversity was affected negatively by low pH and high concentrations of dissolved zinc (Fig. 1), which together explained 66 % of the variation in diversity (Table 2). All sites with pH < 6 or concentration of dissolved zinc > 0.5 mg/L were dominated by 1–2 taxa and had diversity indices less than 1. No other variables, including metal oxide deposition and nutrient concentrations, were significantly related to fungal diversity after the effects of pH and zinc were accounted for.

Ergosterol concentrations ranged from 0.01–0.75 µg/mg AFDM. Ergosterol analysis was problematic at acidic sites (see below), thereby preventing an analysis of effects of mine drainage on concentrations of ergosterol. Rates of respiration ranged from 0.05–0.48 µg O_2 mg $AFDM^{-1}$ h^{-1}. The rate of respiration was negatively related to deposition of metal oxides (Fig. 2). pH and con-

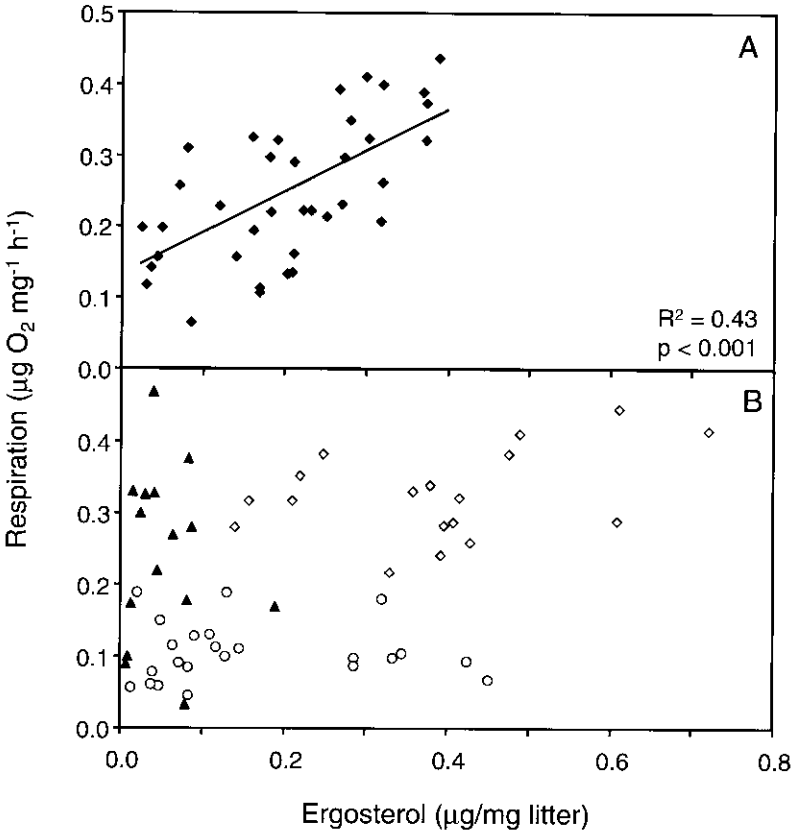

Fig. 3. Rate of respiration versus ergosterol concentration of leaves from pristine sites **(A)** and sites affected by mine drainage **(B)**. Open diamonds represent sites primarily affected by dissolved zinc, open circles represent sites primarily affected by metal oxide deposition, and closed triangles represent sites primarily affected by low pH (<5).

centration of dissolved zinc did not explain significant variation in respiration rate after the effects of metal oxide deposition were taken into account.

The rate of respiration was closely related to the concentration of ergosterol on leaves collected at different times from the 7 pristine sites (Fig. 3 A). This was not the case for leaves from sites affected by mine drainage (Fig. 3 B). The relationship between ergosterol and respiration on leaves depended on the nature of the main stressor (pH, zinc, metal oxide deposition) from mine drainage at a site. Leaves incubated at sites primarily affected by zinc often had high concentrations of ergosterol and rates of respiration similar to those of leaves from pristine sites. Leaves at sites that were primarily affected by metal oxide deposition usually had low rates of respiration, but often had

Table 3. Description of stressors at sites for ergosterol and respiration patterns shown in Figs. 4–6.

Site	Catchment	pH	Zn (mg/L)	Deposition of metal oxides ($g\ m^{-2}d^{-1}$)
UFG	French Gulch	7.7	<0.01	<0.01
LFG	French Gulch	7.5	1.0	<0.01
SM	St. Kevin Gulch	7.3	<0.01	<0.01
SKD	St. Kevin Gulch	4.8	3.5	0.31
LG2	St. Kevin Gulch	2.7	80	<0.01

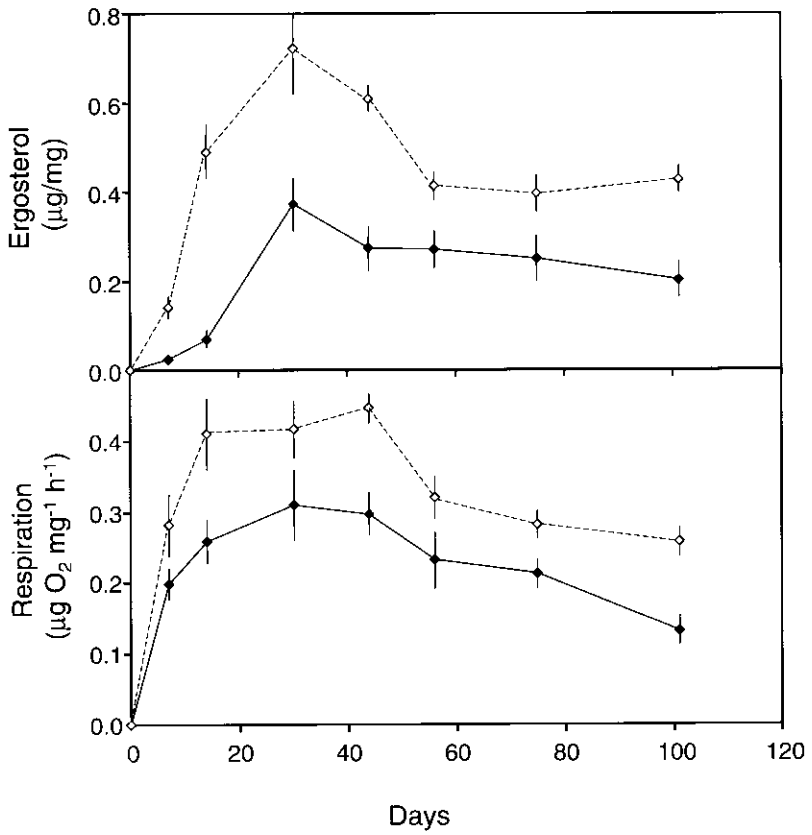

Fig. 4. Ergosterol concentrations and respiration rate of leaves over time from pristine site UFG (solid diamonds and line) and site LFG affected by mine drainage (open diamonds and dashed line). Description of stressors from mine drainage at the sites is provided in Table 3. Values are means ± 1 S.E. (n=3).

high concentrations of ergosterol. Leaves at sites that were primarily affected by low pH often had low concentrations of ergosterol but high rates of respiration.

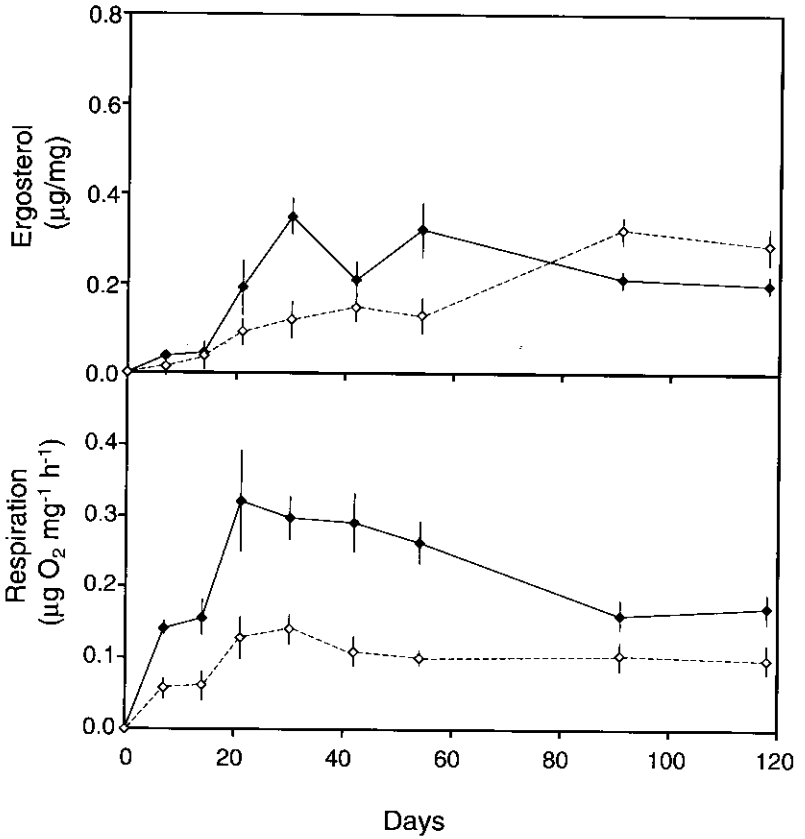

Fig. 5. Ergosterol concentrations and respiration rate of leaves over time from pristine site SM (solid diamonds and line) and site SKD affected by mine drainage (open diamonds and dashed line). Description of stressors from mine drainage at the sites is provided in Table 3. Values are means ± 1 S.E. (n=3).

The relationships between ergosterol and respiration can be seen more clearly by closer examination of selected sites. At pristine sites UFG and SM (Table 3), ergosterol concentrations increased rapidly during the colonization period, then gradually declined (Figs. 4–5). Respiration rate followed a similar pattern, but decreased more sharply than ergosterol over time. Site LFG (Fig. 4) had elevated zinc concentrations (Table 3) compared to the pristine site upstream (UFG). Ergosterol concentrations and respiration rates at LFG were higher than at UFG and other pristine sites.

Site SKD had a moderate concentration of zinc, low pH, and a high rate of metal oxide deposition (Table 3). Ergosterol concentration increased slowly at this site over the course of monitoring (Fig. 5). Respiration rate decreased

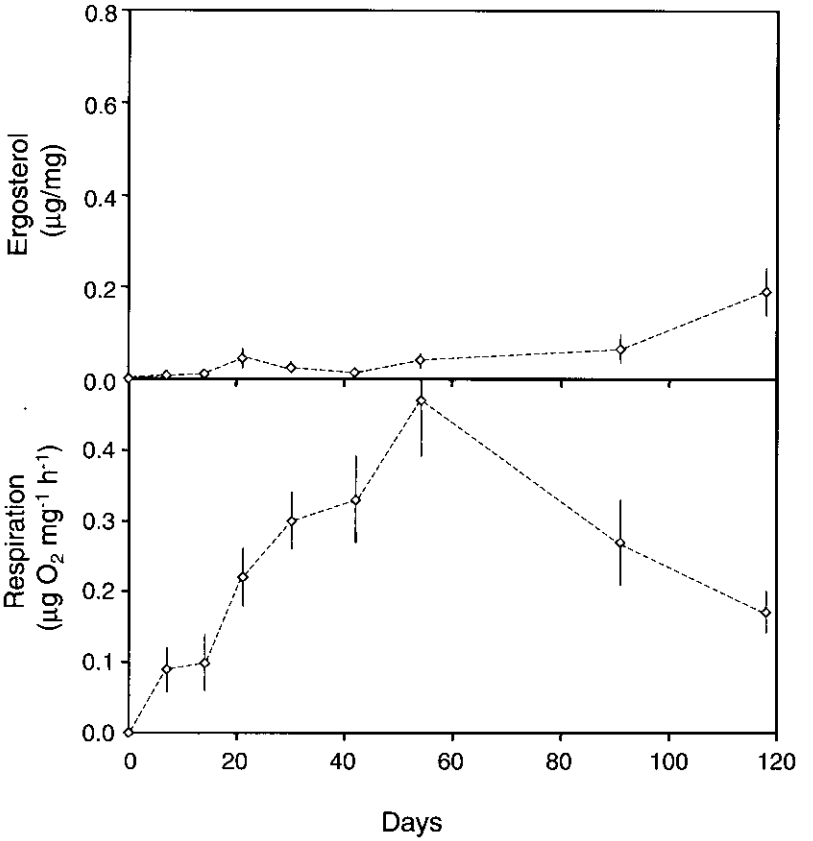

Fig. 6. Ergosterol concentrations and respiration rate of leaves over time from site LG2 affected by mine drainage. Description of stressors from mine drainage at the site is provided in Table 3. Values are means ± 1 S.E. (n=3).

slightly over time after an initial peak, and always was lower than the rate at SM, the pristine site in the same catchment.

Site LG2 had very low pH and a very high concentration of zinc (Table 3). Respiration rate of leaves incubated at LG2 was high, despite very low concentrations of ergosterol (Fig. 6). As at other acidic sites, septate hyphae were visible on the leaves and were culturable on malt extract agar. Although ergosterol peaks were usually small, HPLC chromatograms of leaves from acidic sites had several major peaks with retention times shorter or longer than ergosterol. These peaks were not present in significant amounts in chromatograms of leaves from pristine sites.

Discussion

Aquatic hyphomycetes were common at all pristine sites in our mountain streams. Some pristine sites had fairly high diversity (Shannon-Wiener index >1.5), but others had lower diversity, including one site with an index of 0.87. Common taxa, such as *Lemonniera aquatica*, often dominated the fungal community (>60 % of spore counts) at these sites. In general, our estimates of diversity and the number of species we observed (data not shown) were lower than most studies of streams (e.g., DUBEY et al. 1994, GARNETT et al. 2000). Sites in the present study were at high elevation (around 3000 m) and usually had low concentrations of nutrients (DIN < 60 µg/L; SRP < 5 µg/L). These two factors may have limited diversity at our pristine sites compared to other streams.

Diversity of fungal communities was low in streams receiving mine drainage. Sites with low pH (<6) or high concentrations of zinc (>1 mg/L) had especially low diversity. Low pH usually is often associated with low diversity of fungal communities in streams (IQBAL & WEBSTER 1977, HALL et al. 1980, SHEARER & WEBSTER 1985, CHAMIER 1987, DUBEY et al. 1994), but fewer studies have examined fungal diversity in streams under stress from metals. BERMINGHAM et al. (1996) found fewer species at a site with high concentrations of iron and manganese than at an upstream reference. KRAUSS et al. (2001) found seven species of aquatic hyphomycetes at a site with very high zinc concentration (2600 mg/L), whereas other sites with lower zinc concentrations had slightly more on average.

Stress from low pH and dissolved metals can influence diversity by two mechanisms. Stress may limit the number of species that can survive under such conditions. Our sites with extremely low pH or high zinc concentrations had only a few fungal taxa on leaves. Alternatively, lack of selective feeding by shredders (SUBERKROPP 1992), which can be absent in stressed streams (NIYOGI et al. 2001), may allow one or a few competitive taxa to dominate the fungal community. Sites with intermediate stress from pH or zinc (and no shredders) had more fungal species but usually had one dominant species that composed more than 95 % of the community. Thus, both mechanisms may have accounted for reduced diversity in streams in our study.

The utility of conidia analysis at our study sites was limited by the effects of mine drainage. Because conidia production can be inhibited by high concentrations of metals (ABEL & BÄRLOCHER 1984, CHAMIER & TIPPING 1997), the technique may not be feasible at some sites affected by mine drainage (but see KRAUSS et al. 2001). As an alternative indicator of fungal diversity, a particle plating method (KIRBY et al. 1990) proved useful at our stressed sites. Some sites had aquatic hyphomycetes that were culturable, even though they did not produce conidia upon aeration of leaves. Although culturing can select

for fungi that are inactive in situ, there was good agreement between conidia production and cultures when both methods were applied to leaves from the same site. Novel techniques such as immunoassays (BERMINGHAM et al. 1997) and fluorescent hybridization (MCARTHUR et al. 2001) may improve analysis of fungal communities on litter.

Our measures of respiration probably reflected fungal activity. Fungal communities generally are more important than bacteria in decomposing leaves during the early stages of breakdown (BALDY et al. 1995, WEYERS & SUBERKROPP 1996). Our streams with stressors from mine drainage may not follow this same pattern, but fungi have been found to be less sensitive than bacteria to low pH in soils (PENNANEN et al. 1998) and fungi can tolerate high concentration of metals (e.g., MIERSCH et al. 1997, KRAUSS et al. 2001). Furthermore, epilithic bacterial production in our streams was affected by low pH (NIYOGI et al., unpubl.). Microbial respiration on leaves decreased with increasing deposition of metal oxides, as other studies have also found (SIEFERT & MUTZ 2001). Microbial respiration was less affected by low pH or zinc, even though these stressors were related to lower diversity of fungal communities. Therefore, fungal activity was not always lower at sites affected by mine drainage, despite lower diversity of fungi at such sites.

The concentration of ergosterol and rate of respiration on leaves were closely related at pristine sites. Ergosterol concentrations at pristine sites increased over 2 to 4 weeks and then decreased gradually, as has been reported for other streams (GESSNER & CHAUVET 1994, GRATTAN & SUBERKROPP 2001). At sites such as LFG (Fig. 4) with elevated concentrations of zinc, ergosterol concentrations and respiration rates often were higher than at pristine sites. Some aquatic hyphomycetes are relatively tolerant of zinc and other metals (ABEL & BÄRLOCHER 1984, MIERSCH et al. 1997, KRAUSS et al. 2001) compared to other biota, including most invertebrates (KELLY 1988). Concentrations of ergosterol on leaves at zinc-contaminated sites were the highest we found (up to 750 µg/g AFDM), and similar to concentrations found elsewhere at warmer sites richer in nutrients (e.g., GESSNER & CHAUVET 1994, PAUL & MEYER 1996, GRATTAN & SUBERKROPP 2001). High biomass and respiration at sites with elevated zinc may have been related to the loss of shredding invertebrates, which were not found at sites with elevated zinc (NIYOGI et al. 2001). Invertebrates may constrain fungal biomass and activity by direct consumption and by competing with fungi for litter (BÄRLOCHER 1980). Other studies have found high ergosterol on leaves when shredders are absent (GESSNER et al. 1998).

Ergosterol and respiration were not closely related under two conditions. First, at sites with metal oxide deposition (such as SKD, Fig. 5), respiration was very low despite moderate concentrations of ergosterol. This apparently contradictory response may reflect the mechanism by which metal oxide depo-

sition affects fungi. As metal oxides are deposited onto the streambed and leaf litter, a layer of metal oxides probably hinders access to the leaves by stream fungi. Furthermore, fungal hyphae on the surface of leaves can become covered with metal oxides (D. K. NIYOGI, personal observation) and may no longer be able to decompose the leaves efficiently. Fungal biomass may develop slowly, but the bulk of these fungi may be dead or in a dormant state, as indicated by the low respiration rates. While ergosterol is usually a good indicator of living fungal biomass, ergosterol may not be degraded at these sites because the fungi are not consumed (shredders were usually absent at such sites) and cannot be easily decomposed (because of coating by metal oxide).

A second mechanism that could have decoupled ergosterol and respiration may have been the absence (or low quantities) of ergosterol on leaves at some very acidic (pH <4) sites such as LG2 (Fig. 6), which had high rates of microbial respiration and visible fungi on the leaves. The HPLC chromatograms of leaves from these sites had several peaks around the ergosterol peak that were not found in leaves from pristine sites. These peaks may represent ergosterol-like compounds, such as ergosta-5,7-dienol, which have different HPLC retention times than ergosterol (NES et al. 1989). These compounds, which may be precursors or degradation products of ergosterol, appear to be present in active fungi instead of ergosterol at such acidic sites. Further work is needed to identify these compounds and determine if they may need to be quantified for estimates of fungal biomass at acidic sites.

Conclusions

In a general model of ecosystem response to stress, NIYOGI et al. (in press) proposed that biodiversity of communities is sensitive to anthropogenic stress, whereas biomass and function (production, decomposition) are sustained at low to moderate stress levels and decline only when stress is very high. Our results for fungal communities in streams affected by mine drainage generally support this hypothesis. Fungal diversity was very sensitive to acidity and zinc from mine drainage, but ergosterol (where quantifiable) and respiration remained high even when diversity was low. However, microbial activity did decline under stress from deposition of metal oxides.

Our findings for fungal communities are very similar to algal communities in these streams (NIYOGI et al., in press). Algal diversity was sensitive to low pH and high concentration of zinc, whereas biomass and primary production were often high at such sites. Thus, diversity and function of stream communities appear to respond differently to the distinct stressors imposed by mine drainage. Both microbial activity on leaves and primary production were negatively related to metal oxide deposition in these streams. The applied outcome

of this finding is that remediation of mine drainage must consider the role of metal oxide deposition in addition to the usual focus of dissolved metals.

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