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Effects of Stress from Mine Drainage on Diversity, Biomass, and Function of Primary Producers in Mountain Streams

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Abstract

This paper proposes a hypothesis that relates biodiversity, community biomass, and ecosystem function to a gradient of stress. According to this hypothesis, biodiversity has a low threshold of response to stress, whereas biomass and function are stable or increase under low to moderate stress and decrease only under high stress. This hypothesis was tested by examining communities of primary producers in streams under stress from mine drainage in the Rocky Mountains of Colorado, USA. Mine drainage exerts chemical stress (low pH, dissolved metals) as well as physical stress (deposition of metal oxides) on stream biota. Diversity of primary producers was usually more sensitive to stress from mine drainage than community biomass (chlorophyll *a*) or primary production. Diversity was negatively related to all stresses from mine drainage, but it was especially low in streams with low pH or high concentration of dissolved zinc. Biomass and production were high in streams with only chemical stress, but they were often low in streams with physical stress caused by metal oxide deposition. Stream sites with aluminum oxide deposition usually had very little algal biomass. The rate of metal oxide deposition, presence of aluminum oxides, and pH together explained 65% of the variation in biomass. The rate of net primary production was highly correlated with biomass and had a similar response to stress from mine drainage. Overall, chemical stresses (low pH, high concentration of zinc) generally led to the hypothesized trends in our model of ecosystems under stress. Physical stress (deposition of metal oxides), however, led to variable responses, and often decreased biomass and function even at low intensity, contrary to the original hypothesis. Thus, the nature of ecosystem response to stress may differ for chemical and physical stresses.

Key words: stress; mine drainage; metals; primary production; algae; stream; stressed ecosystems.

Introduction

The effects of stress on freshwater ecosystems have been studied intensively over the last several decades (for example, see Schindler 1987; Levin and others 1989; Howarth 1991; Rosenberg and Resh 1993; Planas 1996; Genter 1996). Although toxicity tests have documented the thresholds of response for individual species to numerous stresses, the effects of stress at the scale of ecosystems remain poorly understood (Cairns 1983; Kimball and Levin 1985). Effects of stress on ecosystem functions, including primary production, decomposition, and nutrient cycling, have been studied recently (Sheehan 1984; Howarth 1991; Pratt and Cairns 1996).

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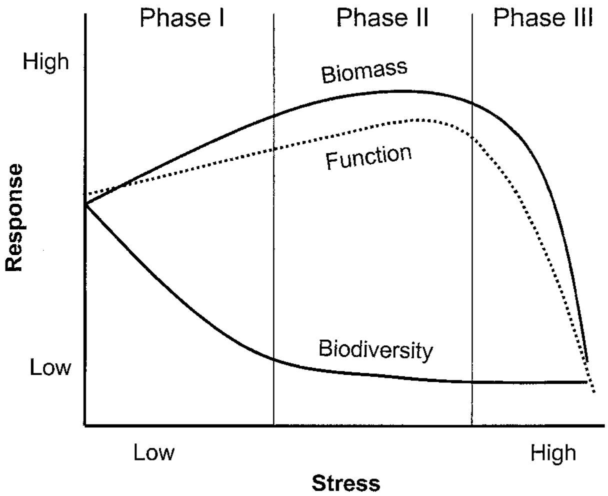

Figure 1. Hypothetical responses of biodiversity, biomass, and function to a gradient of stress.

The mechanisms underlying such effects, however, are still not well described (Levine 1989). In this paper, we propose a general hypothesis relating biodiversity, biomass, and function to stress, and test the hypothesis by examining primary producer communities in streams affected by mine drainage.

Odum (1985) suggested that ecosystem functions would be more robust to change than diversity or other structural measures in ecosystems under stress. Our hypothesis builds on Odum's prediction and a wide range of observations suggesting that the application of stress, even in modest amounts, typically reduces biodiversity, but often without any documentable change in biomass or function (Schindler 1987; Elwood and Mulholland 1989; Howarth 1991). Our hypothesis predicts that as stress is applied incrementally to a system, biodiversity is affected first and biomass second (Figure 1). Changes in function are predicted to follow changes in biomass across a gradient of stress; suppression of function is related to suppression of biomass, rather than to loss of biodiversity.

If our hypothesis is correct, we would expect to find some moderately stressed systems in which biodiversity is partially suppressed but biomass and function are unchanged or even increased (Figure 1). Biomass and function may be stable because tolerant species compensate for the loss of sensitive species by increased biomass and function (Frost and others 1995). This stability would imply that tolerant and sensitive species are functionally similar or redundant (Lawton 1994; Pratt and Cairns 1996; Schindler 1996). Biomass and function may increase with stress because of direct effects, such as stimulation, or indirect effects, such as the suppression of negative ecological feedback. Stimulation may occur when biota are stimulated by the stress, such as certain algae that grow best at low pH (Kelly 1988). Alternatively, indirect effects, such as the suppression of grazing by loss of grazers under stress, may allow greater autotroph biomass to develop than would be found in the absence of stress. Stable or increasing biomass under low stress is designated in Figure 1 as phase I of ecosystem response to increasing stress.

With the progressive application of stress, a second set of conditions (phase II in Figure 1) would involve almost complete suppression of biodiversity, leading to the dominance of one or very few taxa. High rates of function caused by high biomass may still occur at this stage, despite low biodiversity. In a third set of conditions (phase III in Figure 1), biomass and function show suppression under the influence of high stress because even the most tolerant taxa are suppressed by the stress.

Biodiversity is usually sensitive to low levels of anthropogenic stress (Ford 1989; Clements 1991), but stress often fails to suppress ecosystem functions such as respiration or photosynthesis (Odum 1985; Schindler 1987; Clements 1991; Howarth 1991). Thus, empirical evidence is consistent with the general notion that biodiversity and ecosystem function have different thresholds of sensitivity to stress. If this is generally correct, it would explain the confusion in interpretation of empirical data on biodiversity and ecosystem function: Diversity and function simply have different sensitivity thresholds, as indicated in Figure 1.

Numerous studies have recently examined the relationship between biodiversity and function. If diversity and function are positively related (see, for example, Naeem and others 1994; Tilman and others 1997) in stressed systems, biomass and function would decline in conjunction with biodiversity across the gradient of stress (Figure 1). If there is an idiosyncratic relationship between diversity and function (Lawton 1994), biomass and function would be variable across the stress gradient and depend on which taxa are present. Our model is based on a redundancy concept (Lawton 1994), where function is stable given that any species can tolerate the stress.

For the present study, we examined the response of ecosystems to stress in streams affected by mine drainage. Mine drainage, which is common in areas with a history of mining, can impose several distinct stresses on streams: acidity, high concentrations of dissolved metals, and deposition of hydrous metal oxides (McKnight and Feder 1984; Kelly 1988). Acidity is generated by the oxidation of sulfide minerals, such as pyrite, which produces sulfuric acid. Oxidation reactions may occur in mine workings (acid mine drainage) or in naturally exposed sulfide deposits (more generally, acid rock drainage). High concentrations of dissolved metals, including zinc and copper, are often found in mine drainage and can affect the aquatic biota of streams. Some metals, such as iron and aluminum, usually are dissolved in acidic drainage but can precipitate on entering streams. Metals are usually very soluble in acidic water, such as mine drainage, and less soluble at higher pH; metal oxides can precipitate when acidic waters flow into streams of higher pH because pH increases beyond the threshold of solubility for these metals. Metal oxides that precipitate are deposited onto the bed of the stream.

A number of studies have described the algal communities of streams affected by mine drainage (for example, Bennett 1969; Hargreaves and others 1976; Foster 1982; Leland and Carter 1984; Medley and Clements 1998; Verb and Vis 2000). Species diversity is usually lower at sites affected by mine drainage than at pristine sites, but few measurements of biomass are available, and even fewer studies have examined primary production in streams affected by mine drainage (Crossey and La Point 1988). Low pH and metal toxicity often are accompanied by high algal biomass in streams (Elwood and Mulholland 1989; Clements 1991; Planas 1996). However, biota may have different responses to the individual stresses from mine drainage (pH, dissolved metals, deposition of metal oxides) (McKnight and Feder 1984; Niyogi and others 1999, 2001). The goal of our study was to examine the effects of different stresses from mine drainage on diversity, biomass, and production of primary producers and, more generally, to test the hypothesis of ecosystem response to stress.

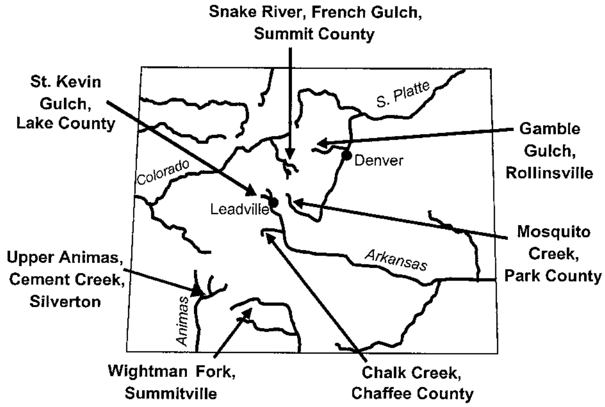

Figure 2. Study regions in Rocky Mountains of Colorado. Study sites (58 total) were situated along multiple streams in each region. Pristine sites were located in each region upstream of mine drainage or in neighboring watersheds.

METHODS

Site Descriptions and Sampling Schedule

Study sites were located on low-order streams at high elevation (2800–3400 m a.s.l.) in the Rocky Mountains of Colorado, USA. Study sites were located in several watersheds (Figure 2) and showed varying effects of mine drainage or natural pyrite weathering. There were 58 study sites overall, 12 of which were pristine (unaffected by mine drainage). Streams usually had slopes of 2%–8%; streambeds were composed mainly of cobble. Study sites were situated in well-lit riffles. Such habitats were the dominant type of habitat in almost all streams.

Streams in the Colorado Rocky Mountains have hydrographs dominated by snowmelt, which occurs predominantly during May and June. Biomass of primary producers is greatly diminished by scour during snowmelt, except for aquatic mosses and liverworts at some sites. Biomass usually increases throughout summer and reaches a peak in late summer to early fall prior to the onset of ice cover. Measurements for this study were timed to coincide with peak biomass during late summer (late August to early September) of 1997.

Abiotic Characteristics of Streams

Procedures for measurement of abiotic variables are described by Niyogi and others (1999). pH was measured with an ion-specific electrode. Water samples for analysis of dissolved metals were filtered through 0.45-μm filters, acidified with ultrapure nitric acid, and analyzed by ICP-AES or AA spectroscopy (Kimball and others 1994). Among dissolved metals, concentrations of zinc were in excess of toxicity standards (USEPA aquatic life criteria) at most sites, whereas concentrations of other metals usually were not. Consequently, zinc was the only metal to be included as a measure of stress from dissolved metals in data analysis.

The rate of metal oxide deposition was measured as the rate of accumulation of deposits on cobbles placed in streams for known periods of time. Cobbles used for this purpose were removed from the stream, brushed clean, and placed in areas of moderate stream velocity (surface velocity 10–30 cm/s). The cobbles were left in the stream for 4–8 weeks, at which time they were removed, placed in plastic bags, and transported to the laboratory. Deposits on the cobbles were brushed into a tared weighing boat for determination of dry and ash mass. Inorganic solids other than metal oxides from mine drainage were not present in appreciable amounts on the cobbles in any streams. The chemical composition of metal oxides from some sites was determined by ICP-AES analysis of acid-digested samples to ensure that the compounds were oxides of iron and aluminum (Niyogi and others 1999). Thus, our measure is of metal oxide deposition and not sedimentation of other kinds of solids. The upper surface area of cobbles was determined by covering with aluminum foil, weighing the foil, and converting to area by use of standardized (100 cm^2) squares (Steinman and Lamberti 1996). Deposition rates (average of three to 10 replicates) were calculated as the mass of ash material per unit of surface area per unit time.

A previous study (Niyogi and others 1999) showed that the type of metal oxide undergoing deposition affects the response of primary producers. We categorized sites as to whether aluminum oxides were present or not and used this variable to explain ecological responses in regression analysis (see below). Metal oxides can be visually distinguished in the field because iron oxides are orange and aluminum oxides are white or gray. The elemental composition of metal oxide deposits at a subset of sites was determined as described above to confirm the predominant metal that was present. In all cases, iron was the predominant metal of orange oxides, and aluminum was the major component of metals in white oxides (data not shown).

Nutrient concentrations were measured in all streams. Water samples for nutrient analyses were filtered through glass-fiber filters (Whatman GF/F, nominal pore size = 0.7 μm) and analyzed by standard protocols (Lewis and others 1984; Wetzel and Likens 1991). Ammonium nitrogen was measured by a phenol hypochlorite colorimetric test; nitrate nitrogen was measured by ion chromatography; soluble reactive phosphorus (SRP) was measured by an acid molybdate colorimetric procedure. Dissolved inorganic nitrogen (DIN) was estimated as the sum of ammonium nitrogen and nitrate nitrogen.

Community Composition, Biomass, and Primary Production

At each site, 10 cobbles were selected at random distances along a longitudinal transect and at random locations across the stream. Cobbles were then used for analysis of community composition, biomass, and primary production as outlined below.

Subsamples of algae and other primary producers were scraped from the cobbles, pooled, and preserved in 5% formalin for identification. Taxa were identified to the genus level, and biovolume estimates from geometric formulas were used to calculate percentage composition of the community (Lowe and Laliberte 1996). From these data, a Shannon-Wiener diversity index was calculated (Hutchinson 1967):

$$H = -\sum_{i=1}^{n} (p_i \cdot \log_2 p_i)$$

where p_i is the proportionate abundance of the *i*th of *n* genera.

Algae and other primary producers (mosses, liverworts) were scraped from the upper surfaces of cobbles and filtered onto glass-fiber filters. Filters were ground with a glass homogenizer, extracted with hot ethanol, and analyzed spectrophotometrically for mass of chlorophyll *a* after correction for phaeophytin (Lewis and others 1984; Wetzel and Likens 1991). The area of the upper surface of the cobbles was determined with a method based on foil wrap (Steinman and Lamberti 1996). Biomass was expressed as the mass of chlorophyll *a* per unit surface area of cobble.

At most sites, cobbles were first used for measurement of primary production by use of recirculating chambers (Bott 1996). Cobbles were placed in acrylic chambers (between 1.0 and 3.5 L total volume), which were filled with stream water and enclosed. Water was recirculated with pumps throughout incubations. Chambers were placed in the stream under full light for 1–2 h; water temperature in the chambers was 10 ± 2°C. Concentrations of dissolved oxygen were measured with a meter (YSI model 58) and were used in estimating rates of net primary production (NPP) as explained by Bott (1996).

Data Analyses

Statistics were performed with SAS software (SAS release 8.00). Correlation coefficients were used to examine general relations among variables. Regression analysis was used to determine the relationships of stress to diversity, biomass, and net primary production. Stepwise multiple regression was used to test the effects of the individual stresses from mine drainage (pH, zinc, metal oxide deposition) and other variables (for example, nutrients) on biological responses. Variables were transformed as necessary to improve consistency with the assumptions of parametric statistical tests. The visual presence or absence of aluminum oxides was included as a categorical variable in some analyses. Because several of the independent variables used in multiple regression were correlated with each other, variance inflation factors (VIF) were calculated using SAS to ensure that collinearity did not greatly affect the results. In all cases reported here, VIF for independent variables was below 2, indicating limited influence of collinearity on the results of the regressions.

A stress index was developed that incorporated the degree of stress from each of the individual stresses associated with mine drainage:

$$\text{Stress index} = \text{St(pH)} + \text{St(Zn)} + \text{St(oxides)}$$

where St(pH) is the stress from pH, St(Zn) is the stress from dissolved zinc, and St(oxides) is the stress from metal oxide deposition. These individual stresses were quantified as follows: St(pH) = 7 − pH, where pH was less than 7. For cases of pH greater than 7, St(pH) was set to zero. St(Zn) = $\log_{10}$(Zn) + 2, where Zn is the concentration of dissolved zinc (mg/L). The detection limit for zinc was set to 0.01 mg/L, which is equal to a St(Zn) of zero. St(oxides) = 2 · [$\log_{10}$(MOD) + 2], where MOD is the rate of metal oxide deposition (g m^{-2} d^{-1}). The detection limit for metal oxide deposition was set to 0.01 g m^{-2} d^{-1}, which is equal to a St(oxides) of zero.

The stress formula sets each of the three stresses (low pH, dissolved zinc, and deposition of metal oxides) to approximately the same scale based on the range of conditions observed at the study sites (each individual stress function varies from 0 to about 4). The formula allows the stresses to be combined into an estimate of overall stress, with which we can test the model shown in Figure 1. The formula assumes that the stresses are additive, but the data for specific agents of stress allow us to separate the effects of the different stresses from mine drainage.

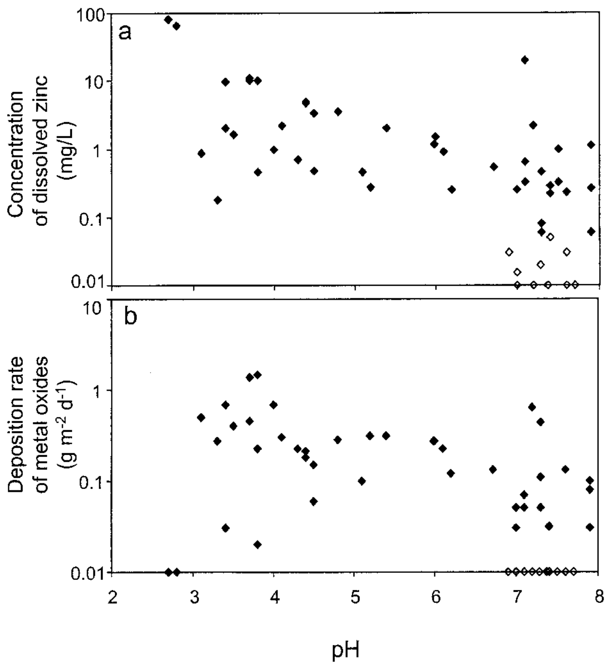

Figure 3. Relations between **(a)** pH and concentration of dissolved zinc (plotted on log scale), and **(b)** between pH and deposition rate of metal oxides (plotted on log scale) across sites. Open symbols represent pristine sites.

Results

Abiotic Characteristics of Streams

Pristine sites had pH values between 7.0 and 7.8. Sites that were affected by mine drainage or natural pyrite weathering had pH values between 2.7 and 7.8. Mine drainage can have circumneutral pH when buffered by carbonates, as was the case for some study sites. Concentrations of dissolved zinc ranged from less than 0.01 to 80 mg/L and were negatively related to pH (Figure 3a). Sites with low pH (less than 4) always had high concentrations of zinc (more than 0.25 mg/L). Sites with circumneutral pH had a large range of concentrations of zinc (up to 20 mg/L). The deposition rates of metal oxides varied from less than 0.01 to over 1 g m^{-2} d^{-1} (Figure 3b). Two sites with very low pH (less than 3) had low rates of deposition, while sites with pH between 3 and 6.5 usually had high deposition rates. Sites with circumneutral pH had a wide range of deposition rates. All pristine sites had circumneutral pH, low concentrations of zinc (less than 0.05 mg/L), and no deposition of metal oxides (open symbols in Figure 3).

Values for the composite stress index ranged from 0 (pristine) to 10.5 (most highly stressed). Sites can be grouped into five main classes on the basis of the main stresses and effects on autotroph communities (Table 1). The average contributions of the individual components of stress to the overall stress index varied in these categories of sites (Figure 4). Sites with stress from metal oxide deposition usually had additional stress from pH and zinc. Five sites had stress only from zinc; five other sites had high stress from low pH and zinc, but lower stress from metal oxide deposition.

Community Composition and Diversity

The Shannon-Wiener diversity index for genera of primary producers ranged from 0.1 to 3.2 across

Table 1. Biomass and Common Taxa of Primary Producers at Five Classes of Sites

Stress	No. of Sites	Biomass (mg ch1 a/m^2) Median	Range	Common taxa[a]
None (pristine)	12	27	6–119	*Achnanthes, Cymbella, Meridian, Hydrurus, Phormidium, Zygnema, Fontinalis*
Aluminum oxides (>0.05 g m^{-2} d^{-1})	15	1.5	<1–19	*Ulothrix, Achnanthes, Phormidium*
Iron oxides (>0.05 g m^{-2} d^{-1})	17	17	<1–110	*Ulothrix, Stigeoclonium, Microthamnion*
Zinc (>0.25 mg/L)	5	75	4–94	*Mougeotia,* unidentified palmelloid chlorophyte
Low pH (<4) Zinc (>0.25 mg/L)	5	85	12–145	*Ulothrix, Eunotia, Scapania*

[a]*Common taxa are those with an average of at least 5% biovolume composition for sites in the category.*

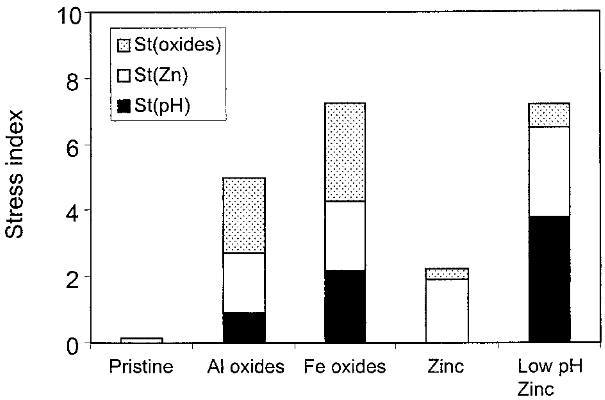

Figure 4. Contributions of individual components of stress (pH, zinc, metal oxide deposition) to the overall stress index in five groupings of sites as outlined in Table 1. Values are means of the stress scores for sites in each category (see Table 1 for number of sites).

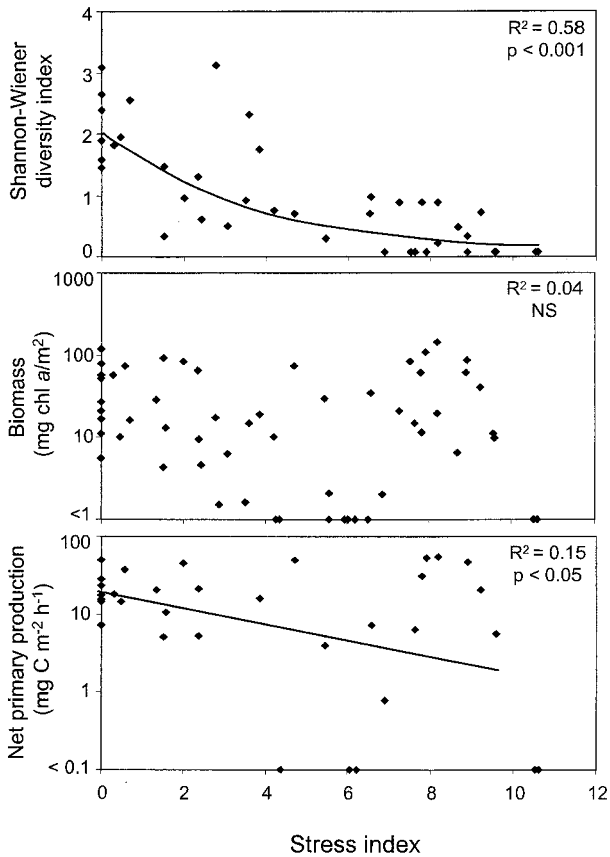

Figure 5. Relations between gradient of stress from mine drainage (stress index calculated as described in Methods) and diversity of genera (Shannon-Wiener diversity index), biomass (cholorphyll *a*), and rates of net primary production. Regression line and statistics for response of diversity are for exponential decrease with stress.

sites. Diversity was negatively related to the stress index (Figure 5) and all three stresses from mine drainage (Figures 6–8). Of the individual stresses, pH and concentration of zinc were highly correlated with diversity, whereas metal oxide deposition was less correlated (Table 2). Metal oxide deposition did not explain significant variation when added to a regression model with zinc and pH, but the presence of aluminum oxides did. Zinc, pH, and the presence of aluminum oxides (as a categorical variable) together explained 66% of the variation in diversity (Table 3).

Each of the five groups of sites based on stresses (Table 1) usually had a characteristic community of primary producers that was found at sites across the study area. The dominant genera at pristine sites included several diatoms (*Achnanthes*, *Cymbella*, *Meridian*), as well as chlorophytes (*Zygnema*) and cyanobacteria (*Phormidium*). At some pristine sites, communities were dominated by *Hydrurus,* while other sites had abundant aquatic mosses (such as

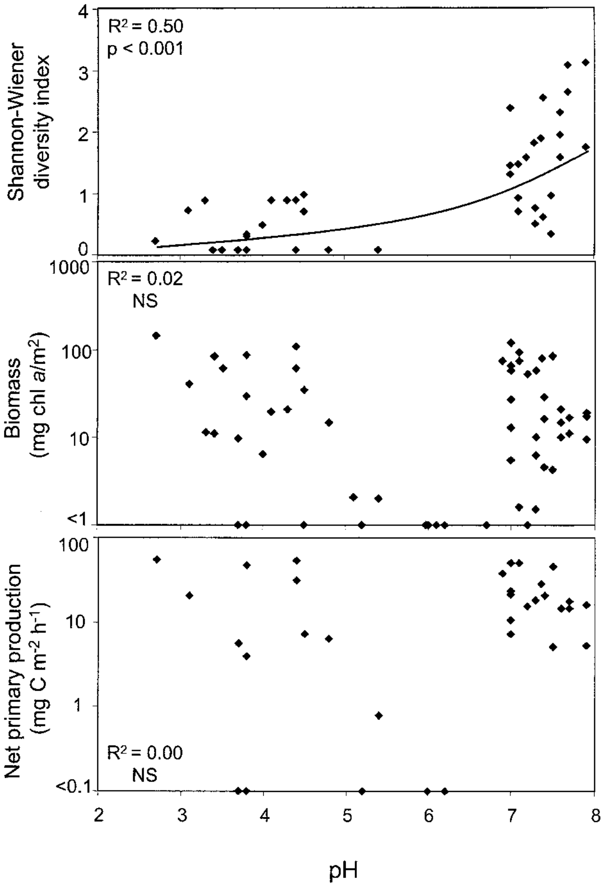

Figure 6. Relations between pH and diversity of genera (Shannon-Wiener diversity index), biomass (cholorphyll *a*), and rates of net primary production. Regression line and statistics for response of diversity are for exponential decrease with stress.

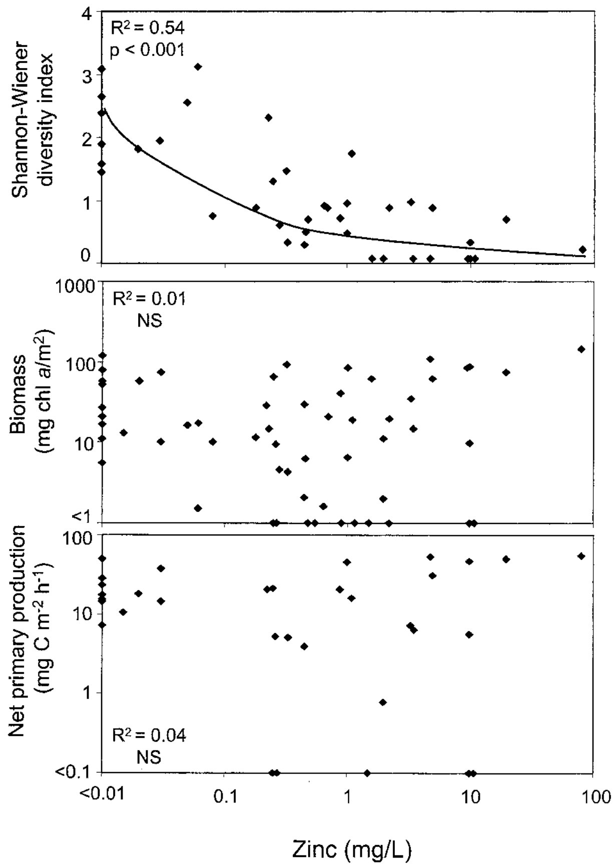

Figure 7. Relations between concentration of dissolved zinc and diversity of genera (Shannon-Wiener diversity index), biomass (cholorphyll *a*), and rates of net primary production. Regression line and statistics for response of diversity are for exponential decrease with stress.

Fontinalis) and liverworts. Sites that had stress only from zinc often became dominated by a single genus of green algae, such as *Mougeotia*. Sites that had significant metal oxide deposition usually had fewer diatom taxa, and were dominated by the chlorophytes *Ulothrix*, *Microthamnion,* and *Stigeoclonium*. Common algae at sites with very low pH (less than 4) included these three chlorophytes as well as acidophilic diatoms, especially *Eunotia*. The acid-tolerant liverwort *Scapania* was found at one site with a pH lower than 4.

Biomass and Primary Production

The biomass of primary producers ranged from less than 1 to 145 mg chl a/m^2 (Figure 5 and Table 1). Most pristine sites (sites with low stress index in Figure 5) with only algae (no mosses or liverworts) had 5–20 mg chl a/m^2. A few pristine sites had higher biomass because of abundant aquatic mosses or liverworts. Two of the pristine sites had abundant algae; one site had extensive growths of the chlorophyte *Zygnema,* and the other had high biomass of the diatom *Didymosphenia*.

Biomass was not significantly related to the composite stress index (Figure 5); sites having similar stress indexes had a wide range of biomass. Of the individual stresses from mine drainage, only metal oxide deposition was significantly related to biomass (Figure 8). Biomass was not significantly related to pH or zinc (Figures 6 and 7). However, pH and zinc explained significant variation in biomass when added to a regression incorporating metal oxide deposition (Table 3). Because acidity (pH) and zinc were correlated with each other, either one (but not both) could be added to a multiple regression model with metal oxide deposition. Acidity and zinc were positively related to biomass after considering the effects of metal oxide deposition (Table 3). The sites with the lowest pH and

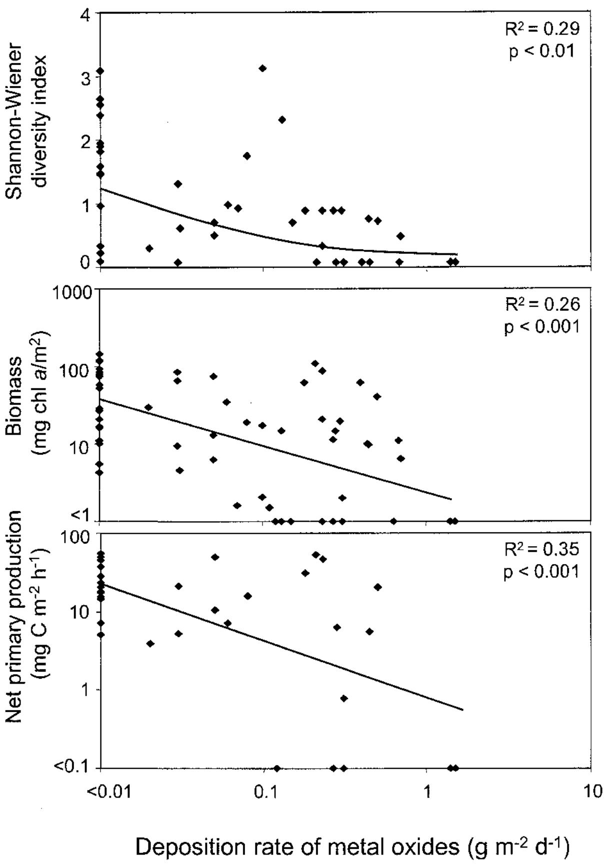

Figure 8. Relations between deposition rate of metal oxides and diversity of genera (Shannon-Wiener diversity index), biomass (cholorphyll *a*), and rates of net primary production. Regression line and statistics for response of diversity are for exponential decrease with stress.

highest zinc often had very high biomass (over 20 mg chl *a*/m^2) (Figures 6 and 7).

Biomass increased with increasing stress index when sites with stress from metal oxide deposition (more than 0.05 g m^{-2} d^{-1}) were excluded from analysis (Figure 9). In fact, all sites with high chemical stress (stress index higher than 4), but little physical stress, had biomass greater than 20 mg chl *a*/m^2.

The presence of aluminum oxides on the streambed explained additional variation when added as a categorical variable to the regression predicting biomass from metal oxide deposition and pH. Sites with aluminum oxides on the streambed had lower biomass. In fact, seven of the 15 sites with deposition of aluminum oxides had less than 1 mg chl *a*/m^2. The presence of aluminum oxides, together with pH and the deposition rate of metal oxides, accounted for 65% of the variation in biomass (Table 3). All sites of pH 5–6.5 had deposition of aluminum oxides and low biomass (Figure 6).

Rates of NPP ranged from less than 0.1 to 54 mg C m^{-2} h^{-1} (Figure 5). NPP was significantly correlated with biomass (Table 1). NPP was negatively related to the stress index (Figure 5). Deposition rate of metal oxides and the presence of aluminum oxides explained 52% of the variation in rates of NPP (Table 3). pH and zinc were not significantly related to NPP rates. As with biomass, sites with the lowest pH or highest zinc had some of the highest NPP rates. We had only a few sites with chemical stress but little physical stress (Figure 9), but these sites had NPP rates similar to pristine sites. NPP and the stress index were not significantly related at such sites.

Stream size (width) and concentrations of nutrients were not closely related to biomass or NPP after the stresses from mine drainage were taken into account. SRP and DIN were not significantly related to biomass after the effects of metal oxide deposition and pH were taken into account.

Discussion

Community Composition and Diversity

Sites that were stressed by mine drainage had characteristic taxa. *Ulothrix*, *Microthamnion*, and *Stigeoclonium* were common chlorophytes in stressed sites and have been found at other sites affected by mine drainage throughout the world (Bennett 1969; Harding and Whitton 1976; Lampkin and Sommerfeld 1982; Spindler and Sommerfeld 1993). *Ulothrix*, which grew in long filaments, was the most abundant algal genus at many stressed sites. Other studies have classified what is probably the same alga as either *Hormidium* (Whitton and Diaz 1981) or *Klebsormidium* (Douglas and others 1998). The diatom genus *Eunotia* also was common at low pH (less than 4) sites in this and many other studies (see, for example, Bennett 1969; Kwandrans 1993; Meegan and Perry 1996; Douglas and others 1998; Ledger and Hildrew 1998; Orendt 1999; Verb and Vis 2000). Certain genera, such as *Ulothrix* and *Eunotia*, are often found at mine drainage sites throughout the world and can be used as indicators of contamination from mine drainage (Whitton 1984; Douglas and others 1998).

Diversity of primary producers decreased with increasing stress from mine drainage. Both low pH and high concentrations of dissolved metals decrease algal diversity in numerous systems (for example, see Elwood and Mulholland 1989; Planas and others 1989; Kinross and others 1993; Olav-

Table 2. Pearson Correlation Coefficients (r) of Variables[a] Used in Data Analysis

	DIN	SRP	Zn	pH	Metal Oxides	Stress Index	SWD	Biomass	NPP
DIN	1								
SRP	**−0.43**	1							
Zn	−0.07	+0.22	1						
pH	+0.27	**−0.49**	**−0.69**	1					
Metal Oxides	+0.01	−0.10	**+0.53**	**−0.51**	1				
Stress Index	−0.12	+0.25	**+0.85**	**−0.88**	**+0.81**	1			
SWD	+0.33	−0.31	**−0.75**	**+0.71**	**−0.53**	**−0.77**	1		
Biomass	−0.25	+0.39	−0.03	−0.07	**−0.51**	−0.18	+0.22	1	
NPP	−0.08	+0.19	−0.20	+0.25	**−0.61**	−0.29	+0.21	**+0.97**	1

DIN is concentration of dissolved inorganic nitrogen; SRP is concentration of soluble reactive phosphorus; Zn is concentration of dissolved zinc; metal oxides is deposition rate of metal oxides; stress index is explained in Methods; SWD is Shannon-Wiener diversity index; NPP is rate of net primary production.
Boldface numbers indicate correlations that are significant at $P < 0.05$ ($n = 58$ for biomass and abiotic variables, 42 for diversity, and 33 for primary production) after Bonferroni correction for multiple comparisons.
[a]All variables were log-transformed except for pH and stress index.

Table 3. Multiple Regression Analysis of Diversity, Biomass, and Primary Production in Relation to Stresses from Mine Drainage

Dependent Variable	df	Overall R^2	Overall *P* Value	Independent Variable	Standardized Regression Coefficient	*P* value
Shannon-Wiener diversity	2, 39	0.66	0.0001	Zn concentration	−0.43	0.0030
				pH	+0.43	0.0033
				Presence of Al[a]	−0.21	0.0382
Biomass (chl a)	2, 55	0.41	0.0001	Rate of deposition	−0.75	0.0001
				pH	−0.47	0.0003
Biomass (chl a)	2, 55	0.33	0.0001	Rate of deposition	−0.67	0.0001
				Zn	+0.32	0.0144
Biomass (chl a)	3, 54	0.65	0.0001	Rate of deposition	−0.54	0.0001
				pH	−0.33	0.0014
				Presence of Al[a]	−0.52	0.0001
Net primary production	2, 30	0.52	0.0001	Rate of deposition	−0.43	0.0039
				Presence of Al[a]	−0.43	0.0043

All variables were log-transformed except for pH and presence of Al.
[a]Presence of Al indicates that aluminum oxides were being deposited at the site.

eson and Nalewajko 1994; Genter 1996; Douglas and others 1998). Two mechanisms can account for low diversity in stressed systems: (a) a small number of taxa, and (b) high abundance of one or a few taxa. In general, high abundance of a few taxa may occur when feedbacks such as grazing are disrupted by stress. In the present study, sites with multiple stresses usually supported only a few genera of algae. Sites stressed only by high zinc in this study supported more taxa but were dominated by one of two chlorophytes (either *Mougeotia* or an unidentified palmelloid chlorophyte), probably because of the loss of grazing invertebrates (see below). Thus, both mechanisms accounted for reduced diversity at stressed sites.

In general, physical stress (oxide deposition) was not as strongly related to decreased diversity as chemical stress (zinc, pH). However, almost all sites with physical stress had some degree of chemical stress, so it was difficult to isolate the effects of physical stress on diversity. In another study, physical stress did not affect diatom diversity in a stream that had deposition of metal oxides (Wellnitz and Sheldon 1995). Further research is needed to elucidate the effects of physical stressors on diversity of autotrophs and other biotic compartments of streams.

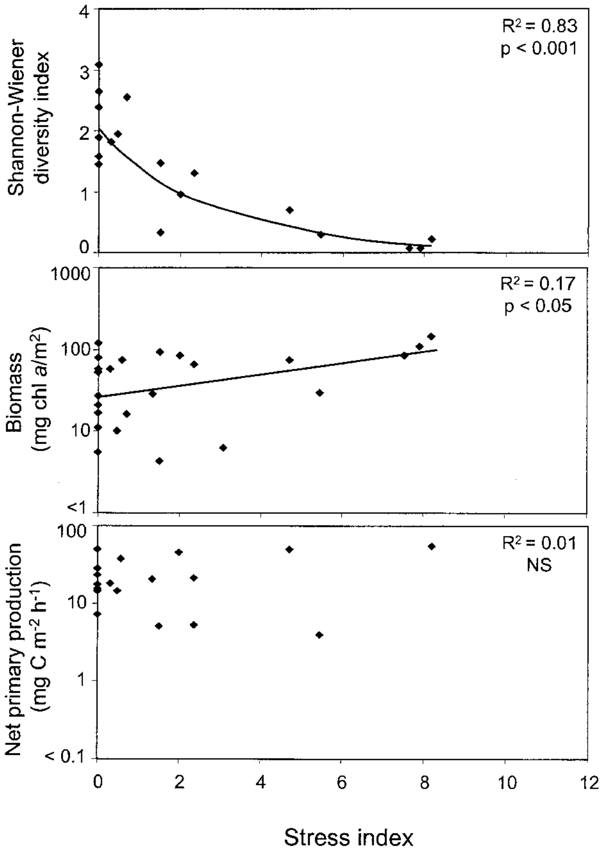

Figure 9. Relations between gradient of stress from mine drainage (stress index calculated as described in Methods) and diversity of genera (Shannon-Wiener diversity index), biomass (cholorphyll *a*), and rates of net primary production for sites with little or no deposition of metal oxides (less than 0.05 g m^{-2} d^{-1}). Regression line and statistics for response of diversity are for exponential decrease with stress.

Biomass and Primary Production

Biomass of algae at our pristine sites was low compared to that of many well-lit streams (Biggs 1996). Nutrient concentrations were usually low at our sites, and extensive growths of filamentous algae were only present at one site. Additionally, herbivory can be an important control on algal biomass (Steinman 1996), especially in mountain streams (Wellnitz and others 1996). Grazing mayflies were abundant at all of the pristine sites in the present study (DK. Niyogi personal observation) and may have suppressed algal biomass in the streams (Biggs and others 1998).

Sites without physical stress from metal oxide deposition had high biomass even under high chemical stress (Figure 8). Other researchers have noted high algal biomass in stressed streams (Mulholland and others 1986; Crossey and La Point 1988; Planas 1996). Grazing insects, such as mayflies, are very sensitive relative to algae to low pH or high concentrations of zinc (Clements 1994; Courtney and Clements 1998; Richardson and Kiffney 2000) and were absent at many stressed sites in the present study (D K. Niyogi personal observation). We hypothesize that the absence of grazing may have contributed to the high biomass of primary producers at the stressed sites.

Few studies have demonstrated the physical effect of metal oxides on stream biota, but Sode (1983), McKnight and Feder (1984), and Wellnitz and Sheldon (1995) all showed low algal biomass in association with the deposition of metal oxides. Metal oxide deposition can limit biomass by two mechanisms: directly, by coating algae as the oxides are deposited from the water column; and indirectly, by coating the substrate and thereby preventing colonization. Both mechanisms occurred in streams of this study. At low deposition rates, algae grew on rocks but became coated with metal oxides. At high deposition rates, algae usually did not grow on rocks that were covered with metal oxides. The growth of *Ulothrix* in association with iron oxides was a notable exception to this pattern and accounted for high biomass at some sites with metal oxide deposition (Figure 8). Streams with high concentrations of suspended sediment can have low algal biomass because of light limitation (Ryan 1991), but streams in our study that were affected by metal oxide deposition had low turbidity.

Niyogi and others (1999) found that aluminum oxides were more detrimental to algae than iron oxides in a stream receiving mine drainage. In the present study, the presence of aluminum oxides explained much of the variation in biomass. The response of biomass and NPP to the stress index (Figure 5) and metal oxide deposition (Figure 8) was variable in large part because of the differential effects of aluminum and iron oxides, which are not well understood (Niyogi and others 1999).

Morin and others (1999) reported that biomass could account for much of the variation in primary production in streams across regions. In the present study, rates of NPP were highly correlated with biomass, and NPP and biomass were affected similarly by stresses from mine drainage. The relationship between biomass and NPP was related to taxonomic composition; several sites that had abundant aquatic mosses and liverworts had lower rates of NPP per unit of biomass than sites dominated by algae (data not shown; compare Arscott and others 1998; Stream Bryophyte Group 1999).

Responses to Stress

We expected diversity to be sensitive to stress from mine drainage (Figure 1). The diversity of algal genera at sites closely matched an exponential relationship to our composite stress index (Figure 5) and to the individual stresses as well. We predicted biomass and function to be stable or increasing across the stress gradient, but this was not the case. Biomass and function responded differently to the individual stresses from mine drainage and were often low at even moderate amounts of physical stress from metal oxide deposition.

Chemical stress caused by low pH, high concentrations of zinc, or a combination of the two generally led to stable or increasing biomass and function (NPP) as predicted by our model (Figure 1). At sites with only chemical stress, biomass increased slightly (but significantly) with stress, while primary production was stable (Figure 8), although we only had data for a few sites of high stress. The predicted pattern of declining biomass and function under high stress (phase III) did not occur, even at sites with the greatest chemical stress. For example, a site with pH of 2.7 and zinc concentration of 80 mg/L still had very high biomass. Phase III may occur, however, under more extreme stress, such as pH less than 2, when even the most tolerant algae cannot persist.

Most descriptions of streams under stress are for chemical stresses, such as low pH or elevated concentrations of dissolved metals, and these studies are consistent with the model shown in Figure 1. Crossey and La Point (1988) reported low diversity but high biomass and production in a stream affected by dissolved metals. Mulholland and others (1986) found higher biomass and aerial primary productivity in acidic streams than neutral references, despite changes in species composition. Medley and Clements (1998) found a significant decrease in diversity of diatoms but no significant suppression in their abundance in metal-contaminated streams in Colorado. In a review of streams affected by acidic deposition, Elwood and Mulholland (1989) reached the conclusion that stressed sites often had increased algal biomass, despite a decrease in diversity. As in the present study, they suggest that a suppression of grazing invertebrates may account for the high algal biomass.

Other aquatic ecosystems appear to follow the same pattern of ecosystem response to chemical stress (deNoyelles and others 1982; Howarth 1991). Schindler (1987, 1990) reported that functional measures, such as primary production, were always more resistant to stress than structural measures, including diversity, in lakes of varying pH. Havens and Carlson (1998) found that phytoplankton and zooplankton biomass remained stable in acidified lakes because of functional complementarity, where tolerant species compensate for the loss of sensitive species (Frost and others 1995). Similarly, Klug and others (2000) noted stable or increasing algal biovolume in experimentally acidified lake mesocosms because of compensation by chlorophytes for the loss of sensitive diatoms. These studies suggest that function is often stable despite a decrease in diversity in chemically stressed ecosystems. Primary production in most aquatic systems is limited by nutrients, such as nitrogen and phosphorus, and concentrations of these nutrients will limit production as long as tolerant species can survive the stressful conditions (Levine 1989).

The effect of biodiversity on ecosystem function has been studied and debated in recent years (see, for example, Naeem and others 1994; Tilman and others 1997; Hooper and Vitousek 1997; Huston 1997). Stressed ecosystems, which often have low diversity, show how function can be maintained at low diversity. Our results, along with other studies on stressed ecosystems cited above, generally support the redundancy concept in that function is stable because increasing abundance of tolerant species compensate for the loss of sensitive species. However, confounding factors can obscure the view of biodiversity–function relations for specific ecosystem compartments (for instance, autotrophs). For example, the loss of grazing and other changes to the trophic structure of stressed streams can have larger effects on autotroph biomass and function than loss of diversity.

Some experimental studies show that algal biomass can be suppressed by small or moderate amounts of chemical stress (for example, see Maurice and others 1987; Hill and others 2000). The use of artificial streams or artificial substrates may account for observations of declines in algal biomass in some stressed systems. Artificial streams may lack a source of stress-tolerant taxa. Additionally, some stress-tolerant taxa, including certain filamentous chlorophytes, do not grow well on artificial substrates, especially during short-term monitoring. An advantage of studying streams affected by mine drainage is that these streams have usually been in a stressed state for many years or even decades, and biomass is probably not limited by the colonization of tolerant species.

The response of biomass and primary production to physical stress from mine drainage did not match the predictions shown in Figure 1. Deposition of metal oxides usually decreased biomass and function but not diversity. This result was complicated by the especially strong effect of aluminum oxides on biomass and production. Physical stress caused by metal oxide deposition coincides with low algal biomass in the few relevant studies (Sode 1983; McKnight and Feder 1984; Wellnitz and Sheldon 1995). Other physical stresses, such as sedimentation, also can decrease algal biomass (Lenat 1984; Ryan 1991). Further research is needed to clarify the effects of physical stresses on ecosystem properties such as diversity, biomass, and function.

Our results relied on multiple regression analyses using several independent variables. Because the independent variables were sometimes correlated with each other (Table 2), we could not always isolate the effects of certain stressors from others. For example, zinc was usually high at low pH, and either variable (but not both) could be added to metal oxide deposition in a regression explaining biomass. However, we could discern other effects of the stresses from mine drainage because we had a large number of sites with substantial variation in the amounts of the stresses. For example, we had several sites with stress from pH and zinc but not from metal oxide deposition, which allowed us to differentiate the effects of chemical and physical stresses on biomass and function.

The different ecological responses to chemical and physical stresses also limited the use of our stress index for describing conditions in streams affected by mine drainage. The specific stressors at a given site would affect the composition as well as the biomass and function of the autotroph communities. Similar indexes of stress from the combined effects of dissolved metals have proven useful in some studies (for example, Clements and others 2000). However, the variable response of stream autotrophs to physical stress from metal oxide deposition led to high variation in the ecological response to our stress index.

Conclusions

The effects of mine drainage on biomass and primary production in our study streams are summarized in Figure 10. Biomass is negatively affected by deposition of metal oxides, especially aluminum oxides. Sites with low pH or high zinc usually have low diversity of primary producers, but they often have high biomass if the deposition rate of metal oxides is low. Biomass is positively related to low pH and elevated zinc, probably through an indirect effect on grazing invertebrates, especially mayflies.

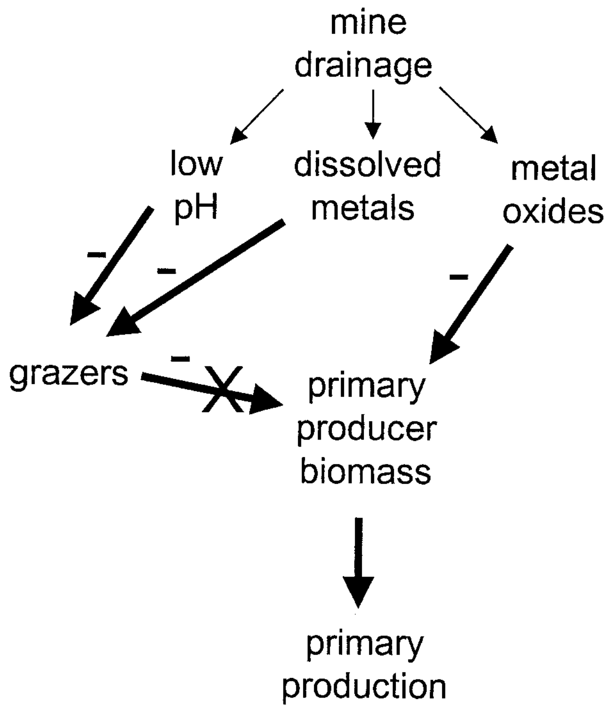

Figure 10. Conceptual model of how mine drainage affects primary production. Mine drainage exerts three stresses on stream biota; deposition of metal oxides is the main stress affecting biomass of primary producers. Grazing by invertebrates, which normally limits biomass in mountain streams, can be disrupted by mine drainage, resulting in the loss of this feedback on biomass. Rates of primary production are determined primarily by biomass.

Finally, the rate of primary production is closely related to the biomass of primary producers.

The differential effects of stresses from mine drainage reported here and elsewhere (McKnight and Feder 1984; Niyogi and others 2001) have implications for remediation of mine drainage because treatment should focus on the stresses that limit biota and ecosystem functions. Remediation is often focused on reducing concentrations of dissolved metals that affect survival of invertebrates and fish. Additionally, remediation must decrease the deposition of metal oxides, which can affect primary producers and higher trophic levels.

Streams affected by chemical stresses from mine drainage followed the predicted patterns of declining diversity accompanied by stable biomass and function across a gradient of stress. Physical stress from mine drainage, on the other hand, decreased biomass and function. The differences in ecosystem response to chemical and physical stresses may account for some of the variability reported in other studies on mine drainage and other stresses.

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