Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A.

G. Wayne Minshall, Christopher T. Robinson, and Deron E. Lawrence

Abstract: Wildfire is a major large-scale disturbance affecting terrestrial landscapes and lotic ecosystems in many regions of the world. We examined environmental and biological responses of 20 streams in Yellowstone National Park, U.S.A., over 5 years following extensive wildfires in 1988. Streams of burned catchments displayed increases in dissolved nitrate-nitrogen following the fires. Summer water temperatures often exceeded 20°C in small (first- and second-order) streams of burned catchments compared with <15°C in their unburned counterparts. Habitat heterogeneity decreased in streams of burned watersheds as demonstrated by changes in substrate embeddedness and near-bed velocities. Substantial alteration of channels and major restructuring and movement of large woody debris occurred in fire-impacted but not reference streams. Transported and benthic organic matter, mostly charcoal, increased in burned sites. No major changes were found in macroinvertebrate density, biomass, or richness, although significant changes occurred in relative abundances of miners, gatherers, and scrapers of burned sites. Chironomidae abundance was greater initially (postfire years 1–3), followed by later increases (postfire years 3–5) by the mayfly *Baetis bicaudatus* in burned sites compared with reference streams. Our findings demonstrate an integral relationship over time between a stream and its catchment, following large-scale disturbances such as wildfire.

Résumé : Les incendies de forêts constituent une grave perturbation à grande échelle pour les paysages terrestres et écosystèmes lotiques de nombreuses régions du monde. Par suite d’importants incendies de forêts qui ont sévi en 1988 dans le Parc national Yellowstone aux États-Unis, nous avons examiné sur 5 ans les réactions environnementales et biologiques de 20 cours d’eau. Nous avons constaté que les cours d’eau des bassins hydrographiques touchés par les feux présentaient des augmentations de l’azote et des nitrates dissous. De plus, la température estivale des petits cours d’eau (de premier et de second ordre) des bassins brûlés dépassait fréquemment 20°C, alors qu’elle est souvent <15°C dans les autres cours d’eau. Des changements dans la disposition du substrat et dans les vitesses du courant près du fond du lit reflètent une diminution de l’hétérogénéité des habitats dans les cours d’eau des bassins brûlés. Toutefois, des modifications importantes des chenaux ainsi qu’une restructuration et un déplacement de grande ampleur des gros débris de bois se sont produits dans les cours d’eau des régions brûlées, contrairement à ce qui s’est passé dans les cours d’eau de référence. La quantité de matière organique transportée et accumulée, essentiellement du charbon, a augmenté dans les sites brûlés. Nous n’avons constaté aucun changement dans la densité, la biomasse ou la richesse des macroinvertébrés, quoique d’importants changements se soient produits dans l’abondance relative des fouisseurs, des récolteurs et des déposivores des sites brûlés. Dans les trois premières années suivant le feu, les chironomidés étaient plus abondants dans les sites brûlés que dans les sites de référence; dans les deux années qui ont suivi, l’abondance de l’éphémère *Baetis bicaudatus* s’est accrue. Nos résultats démontrent l’existence d’un rapport temporel intégral entre un cours d’eau et son bassin hydrographique par suite d’une perturbation à grande échelle telle qu’un incendie de forêt.
[Traduit par la Rédaction]

Introduction

Globally, wildfire is one of the primary natural disturbances influencing the heterogeneity, patchiness, and diversity of terrestrial landscapes and the lotic ecosystems that drain these landscapes (White and Pickett 1985; Resh et al. 1988). Wildfire profoundly alters terrestrial systems and potentially sets the stage for future successional trajectories and ecosystem development (sensu Kay 1991). Wildfire management has important ramifications towards maintaining biodiversity of terrestrial and aquatic systems and the resulting stability and integrity of these ecosystems (Knight and Wallace 1989; Romme and Despain 1989). Thus, the paucity of information on the effects of wildfire on terrestrial and especially freshwater ecosystems is surprising (Minshall et al. 1989). Indeed, most papers examining fire effects on lotic systems have focused on changes in abiotic properties (flow, sediment, chemistry) (Tiedemann et al. 1979; Bayley et al.1992; Beaty 1994; Ewing 1996), with fewer studies addressing the response of biota (fish and macroinvertebrates) (Albin 1979; Richards and Minshall 1992; Minshall et al. 1995; Roby and Azuma 1995; Mihuc et al. 1996).

The effects of fire on stream ecosystems can be partitioned into (1) short-term (<1 year) changes arising directly from increased water temperatures and abrupt alterations in water chemistry and food quality and (2) delayed responses, including

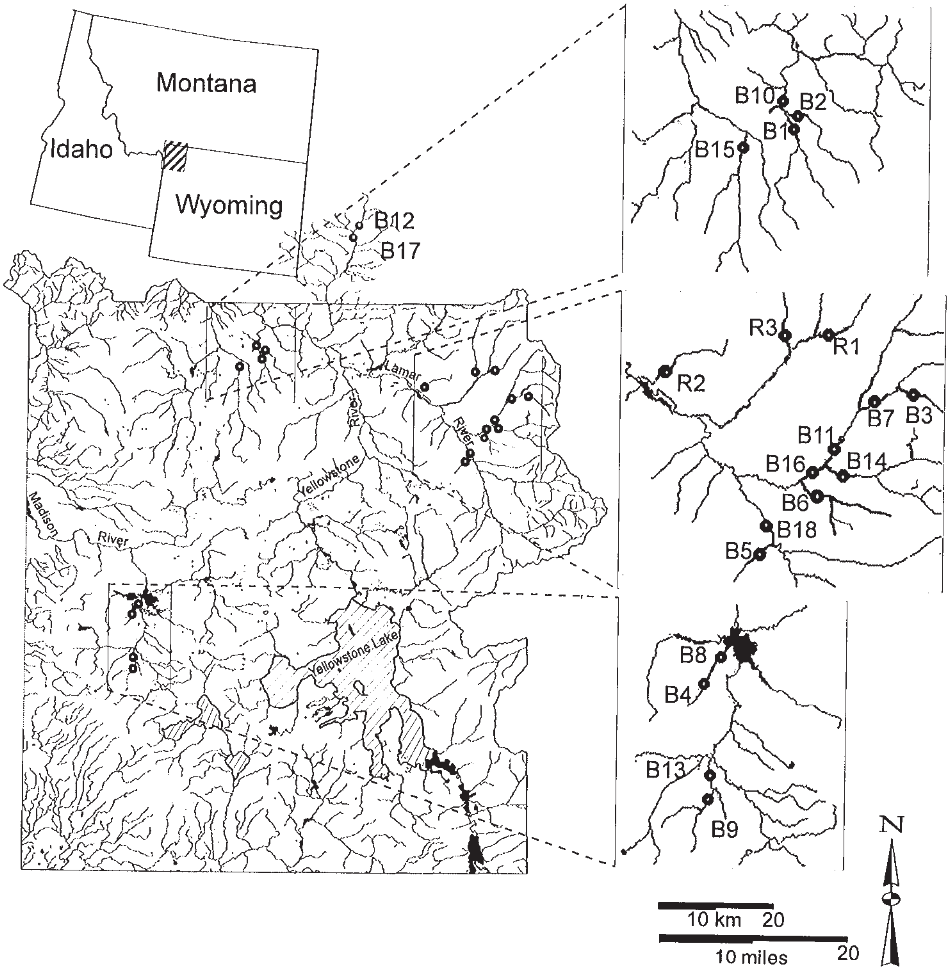
Received July 8, 1996. Accepted April 9, 1997.
J13539

G.W. Minshall,[1] C.T. Robinson,[2] and D.E. Lawrence. Stream Ecology Center, Department of Biological Sciences, Idaho State University, Pocatello, ID 83209, U.S.A.

[1] Author to whom all correspondence should be addressed. e-mail: minswayn@isu.edu

[2] Present address: Department of Limnology, Swiss Federal Institute of Environmental Science and Technology (EAWAG), Überlandstrasse 133, CH 8600 Dübendorf, Switzerland.

Fig. 1. Map of Yellowstone National Park and respective study sites. R, reference site; B, burned site. See Table 1 for stream number designations.



chemical, resulting from the removal and eventual successional replacement of the vegetative cover in stream catchments (Minshall et al. 1989; Minshall and Brock 1991). Delayed impacts can be separated further into midterm (~1–10 years) and long-term (>10 up to 100–300 years) effects. Our study addressed the short-term and midterm effects of fire on stream ecosystems following the conflagration of 1988 in Yellowstone National Park.

Most postfire effects are primarily attributed to physical disturbances associated with increased runoff and sediment scouring and are expected to exert their maximum influence within the first few years after fire, during the initial recovery of terrestrial vegetation. In addition, long-term changes in abiotic and biotic properties of lotic systems (i.e., alterations in food resources and retention capacity in fire impacted streams) are posited to reflect the subsequent recovery of riparian and upland terrestrial vegetative cover following wildfire (Molles 1982; Minshall et al. 1989). This study is one of the few systematic investigations of a landscape-level disturbance of stream ecosystems at a spatial scale of entire catchments and expected recurrence frequency of hundreds of years (Romme 1982; Reice et al. 1990). We focused on ecosystem properties that encompassed benthic macroinvertebrate communities, food resources (periphyton and benthic organic matter), water chemistry (including potentially limiting nutrients), and physical factors that would act as indices of stream ecosystem response to wildfire.

Description of study area and sites

The Greater Yellowstone Ecosystem has two distinct climates (Despain 1987): one type, commonly associated with the interior region and large valleys, has a spring peak in precipitation; the other, found on the western plateaus and the mountains of the northern and eastern parts, has a winter peak in precipitation. These two climates are reflected in the vegetation. Typical valleys are covered by dry grasslands and sagebrush (*Artemisia tridentata*) steppe communities. Douglas-fir (*Pseudotsuga menziesii*) is found on north-facing slopes (Despain 1987). In contrast, mountain areas usually are vegetated by conifer forests, especially Engelmann spruce (*Picea engelmannii*), or moist meadows. Most of our study sites were in areas of montane climate, but a few (Fairy Creek, Iron Springs Creek) were in the interior-type climate (Fig. 1). In Yellowstone, 75–85% of the precipitation occurs as snow or rainfall on snowpack; freezing air temperatures can occur in any month (Despain 1987).

We concentrated our efforts on 20 streams that ranged in

Table 1. Coordinates and physical and chemical characteristics of streams examined in the study.

Stream	Map no.	Order	Coordinates	Catchment area (ha)	% catchment burned	Slope	Discharge (m^3/s)	Median substratum size (cm)	Near-bed velocity (cm/s)	Specific conductance (µS/cm)	pH	NO_3 (mg/L)	Ortho-P (mg/L)
Blacktail Deer, EF	B2	1	110′35″, 44′53″	1 281	92	2.0	0.031	7.5	0.15	126	8.4	<0.002	0.130
Blacktail Deer, WF	B1	1	110′35″, 44′53″	1 570	90	7.0	0.028	4.3	0.17	136	8.5	0.006	0.160
Fairy	B9	1	110′52″, 44′32″	428	76	1.0	0.054	0.1	0.25	66	8.1	0.008	<0.005
Twin	B5	1	110′10″, 44′48″	1 020	68	11.0	0.076	10.3	0.11	190	8.6	0.026	0.057
Upper Cache	B7	1	110′03″, 44′51″	138	64	10.0	0.001	5.3	0.04	153	8.0	0.230	0.180
Blacktail Deer, main	B10	2	110′35″, 44′53″	3 298	88	4.0	0.098	9.9	0.39	136	8.3	0.004	0.078
Fairy	B13	2	110′51″, 44′33″	1 199	81	0.5	0.092	0.4	0.07	318	9.3	<0.002	0.014
Upper Cache	B6	2	110′05″, 44′49″	377	71	10.0	0.004	4.7	0.11	132	8.2	0.008	0.150
Lower Cache	B3	2	110′05″, 44′50″	781	47	9.0	0.011	5.9	0.18	220	8.4	0.111	0.281
Iron Springs	B3	2	110′52″, 44′26″	615	41	14.0	0.065	3.3	0.22	48	7.8	0.019	0.013
Amphitheater	R1	2	110′04″, 44′56″	2 535	2	6.0	0.077	6.7	0.29	82	8.1	0.004	0.067
Rose	R2	2	110′13″, 44′54″	2 390	0	8.0	0.009	6.1	0.14	207	8.5	0.006	0.026
Cache	B11	3	110′04″, 44′51″	12 052	68	2.0	0.184	6.4	0.10	86	8.1	0.040	0.057
Hellroaring	B12	3	110′04″, 44′50″	3 975	59	3.0	0.101	7.7	0.12	85	8.2	0.002	0.041
Lava	B15	3	110′38″, 45′56″	8 968	47	2.0	0.622	30.5	0.44	72	7.8	0.041	0.022
Iron Springs	B4	3	110′38″, 45′56″	1 838	39	1.0	0.656	3.6	0.48	64	7.9	0.004	0.008
Cache, SF	B14	3	110′04″, 44′50″	5 781	39	3.0	0.174	5.5	0.13	105	7.9	0.004	0.095
Pebble	R3	3	110′07″, 44′56″	5 888	17	3.0	0.224	9.9	0.19	203	8.3	0.002	0.008
Cache	B16	4	110′05″, 44′50″	17 995	59	2.0	0.336	9.5	0.21	89	8.1	0.002	0.063
Lamar	B18	4	110′08″, 44′48″	NA	50	1.0	0.58 1	8.5	0.21	155	8.7	<0.002	0.069
Hellroaring	B17	4	110′23″, 45′09″	6 640	46	2.0	0.067	8.5	0.10	83	8.3	0.004	0.039

Note: Physical and chemical data recorded October 1988. Catchment size and percent catchment burned determined from GIS analysis. See Fig. 1 for map number. B, burned stream; R, reference stream.

size from first through fourth order (Table 1). Few catchments having streams larger than fourth order were affected directly by the fires in the Greater Yellowstone Ecosystem. The proportion of the catchment burned for each stream was estimated using GRASS 3.0, a Geographical Information System (GIS). However, about 10% of the burned areas were not registered using the GIS because understory burns are not detected by satellite imagery. Based on the GIS results, most sites had at least 40% of their catchment burned, although the range was from 0% at Amphitheater Creek to 92% for the east fork (EF) of Blacktail Deer Creek (Table 1). Smaller burned sites (first-order average = 78%) typically had a greater proportion of their catchment burned than larger streams (fourth-order average = 52%). Streams showing little of their catchment burned (e.g., <20%) were selected as reference sites.

Most small streams had higher gradients (usually >5% slope) than larger study streams (always <3% slope) with the exception of second-order Fairy Creek (Table 1). Discharge values reflected stream order and catchment area; upper Cache (first order) had the lowest flow (0.001 m^3/s) and Lamar the greatest flow (0.581 m^3/s). In general, low-gradient systems (e.g., Fairy and Iron Springs creeks) had smaller substrate particle sizes than high-gradient systems, although median substrata size was between 5.0 and 10.0 cm for most study streams. Exceptions included the Fairy Creek sites, with substrata consisting primarily of sand and pebbles, and Lava Creek, having mostly large particles (median size = 30.5 cm) of volcanic origin. Average near-bed velocities were lowest in first-order upper Cache (0.04 cm/s) and highest in third-order Iron Springs (0.48 cm/s). Most sites exhibited mean near-bed velocities between 0.10 and 0.20 cm/s (Table 1).

Methods

The sampling protocol focused on factors that would provide both a measure of the short-term impact (first 12 months) and a foundation for subsequent study of the mid- and long-term responses of stream ecosystems to wildfire. Consequently, most of our methods are routine in stream ecology and are described in detail in standard reference sources (Talling 1973; Weber 1973; Greeson et al. 1977; Lind 1979; Platts et al. 1983; Merritt and Cummins 1984; APHA 1989). Details for relatively nonroutine procedures completed each year are given below.

Five permanent transects were established at approximately 50-m intervals at each study site to measure channel morphology and riparian conditions over time. The location of the initial (monumented) transect at each site was predetermined from topographic maps and aerial reconnaissance. Annual temperature ranges (delta-T_{ann}) were obtained using minimum and maximum temperature recorders placed in each stream in September 1988. At sites where temperature recorders were lost between sampling occasions, delta-T_{ann} was estimated using the maximum water temperature at the time of sampling and the minimum temperature based on available evidence (e.g., ice cover). Most of the routine sampling occurred during baseflow conditions. Chemical measures recorded when sampling at each site included specific conductance (Orion model 250) and pH (Orion model 125). In addition, water samples were collected, stored on ice after respective preservation, and analyzed in the laboratory for alkalinity, total hardness, nitrate, and orthophosphorus using standard methods (APHA 1989).

Field maps of woody debris were drawn to scale for two 50-m reaches at each site beginning in 1988. All wood larger than 40 cm long or 2 cm in diameter was recorded each year. The number of pieces present each year was tallied from the debris maps and the amount of wood rearrangement summarized by counting the number of pieces lost or gained in each subsequent year. Substratum size (*y*-axis) and percent embeddedness were determined for 100 random observations distributed throughout a 200-m reach at each site (Leopold 1970; Platts et al. 1983). Embeddedness was visually estimated as the degree (nearest quartile percent) of interstitial filling of the substratum by fine particles (sand and silt). Water velocities (Ott C-1 current meter) near the stream bed and water depths also were recorded at these 100 random locations, although depths were not measured in 1990. Discharge also was calculated for each site at the time of sampling (Bovee and Milhous 1978).

Quantitative samples of periphyton were collected from rock substrata near each transect ($n = 5$ per site per sample date) (after Robinson and Minshall 1986) and analyzed for chlorophyll *a* and ash-free dry mass (AFDM) (Lorenzen 1966; Stockner and Armstrong 1971; APHA 1989). Transported organic matter (TOM) was collected using sets of nested-nets ($n = 2$ per site per sample date), separated into coarse particulate organic matter (CPOM, >1.0 mm) and fine particulate organic matter (FPOM, 0.52–1.0 mm) fractions, and quantified as AFDM. TOM was not collected at several third- and fourth-order sites in 1990 due to high runoff from a rainstorm. Benthic macroinvertebrates were sampled from one location near each transect ($n = 5$ per site per sample date) using a modified Surber sampler (mesh size = 250 μm) following procedures described in Platts et al. (1983). Benthic macroinvertebrates were hand-picked from each sample and identified to the lowest taxonomic unit feasible using a dissecting microscope at 10×. We evaluated among-year changes in density, biomass, species richness, and functional feeding groups (after Merritt and Cummins 1984) of macroinvertebrates. Benthic organic matter (BOM) collected in conjunction with the sampling of macroinvertebrates was quantified as AFDM. Prior to quantification, the percent charcoal (nearest quartile) of each TOM and BOM sample was estimated visually from dried samples spread on white paper.

Temporal change in stream habitat conditions was examined using summed among-year coefficients of variation (CVs) for important physical measures (e.g., see Robinson et al. 1994). Among-year CVs for these variables were derived from either annual averages (e.g., substrate size, water velocity, depth) or individual spot measures (i.e., chemical constituents). We used these data to test the hypothesis that streams experiencing major habitat changes over time would have greater CVs than streams showing less environmental change over time. Changes in the spatial heterogeneity of benthic habitats were assessed by comparing annual CVs for specific habitat measures (substrate size and embeddedness, near-bed velocities, water depth) among study years. Here, we posited CVs to either increase or decrease over time depending on the measure of interest. For summary purposes, streams were grouped by date and stream order with selected variables and then compared among dates for each stream order using ANOVA followed by Tukey’s post hoc test (Zar 1984). When necessary, variables were transformed either $\log(x + 1)$ or arcsine(square root(x)) prior to statistical analysis to meet the assumption of normality (Zar 1984). Variables that still failed to meet the assumption of normality were analyzed using the nonparametric Kruskal–Wallis rank test followed by Dunn’s mean comparison test (Zar 1984). Although this study encompassed a relatively large number of study streams, budgetary limitations restricted the number of reference streams to three, thus constraining some statistical inferences in the text. Further, readers are referred to Minshall and Robinson (1995) for additional data on individual stream response.

Results

Physical and chemical characteristics

Weather records for Yellowstone National Park are limited, and continuous flow records were available only for lower Blacktail Deer Creek. We present here the available prefire and postfire discharge records (U.S. Geological Survey; no data for 1946–1988) for Blacktail Deer Creek and the corresponding precipitation data (U.S. Weather Bureau) for the nearest recording station in Livingston, Mont. (Fig. 2). Winter–spring precipitation and total annual precipitation were similar between pre- and postfire years, although being slightly wetter before than after the fire. Baseflow and peak discharge also appeared comparable for the two data sets. In contrast, annual discharge was somewhat greater and the period of high flow associated with spring snowmelt runoff and its peak occurred earlier in the spring following the fires (Fig. 2).

Data collected in 1988 prior to any major runoff was used to characterize the initial chemical and physical conditions at a site. The water chemistry varied widely among study streams and reflected local geological conditions (Table 1). For example, second-order Fairy Creek showed higher specific conductance, pH, and alkalinity than all other sites as a result of geothermal inputs. Larger streams (fourth-order sites) exhibited less chemical variation than smaller sites, most likely due to the homogenizing effects of greater flow. Instream nitrate concentrations under baseflow conditions were <0.004 mg/L for most sites; notable exceptions included first-order upper and second-order Cache creeks. Instream phosphorus levels under baseflow conditions typically were <0.10 mg/L, although higher levels (>0.10 mg/L) were observed in the smaller Cache and Blacktail Deer creeks.

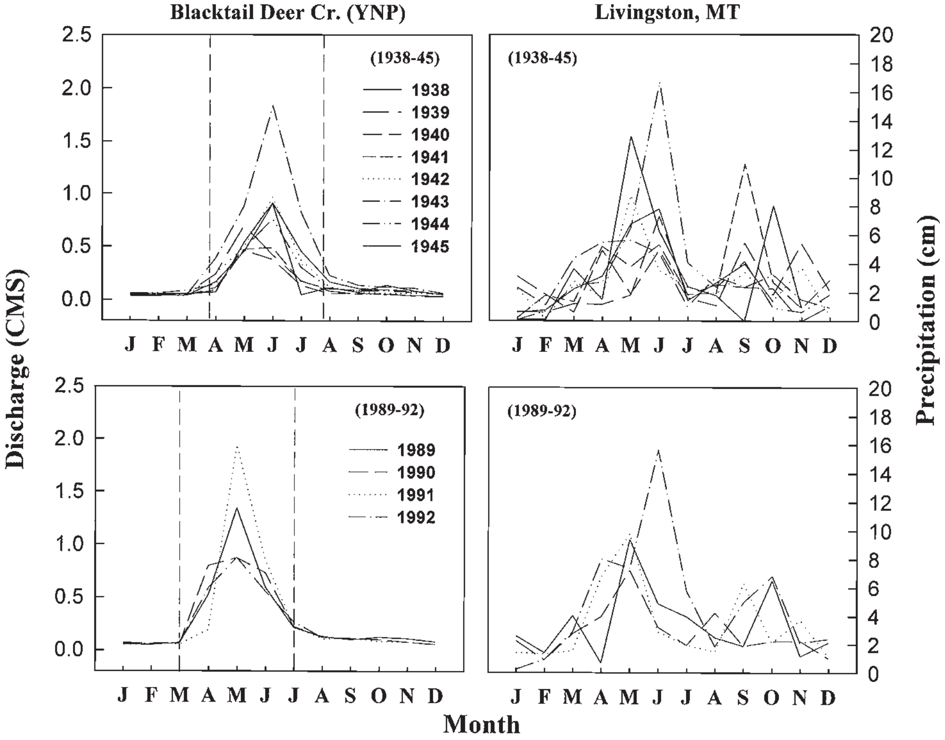
Although useful in characterizing the chemical conditions in the burned and reference streams, our data do not adequately reflect conditions during periods of runoff when elevated concentrations of some ions are expected. For example, pronounced pulses of nitrate and phosphate associated with snowmelt and precipitation were observed in several burned sites following the Yellowstone fires, including Cache and Blacktail Deer creeks (P.D. Sebesta, NASA Ames Research Center, Moffelt Field, Calif., personal communication). Concentrations at these times reportedly exceeded 0.5 mg/L for phosphate and 1–2 mg/L for nitrate and extended throughout the mid-June to mid-September 1990–1993 study period.

Maximum water temperatures were greater ($P < 0.01$) in first- and second-order burned sites than in reference streams and often surpassed tolerance levels of salmonids (i.e., 20°C) (Fig. 3). Average maximum water temperatures were >20°C in second-, third-, and fourth-order burned sites but <20°C in reference streams. Larger burned sites (i.e., third and fourth order) displayed average maximum temperatures comparable with the third-order reference stream, although third-order Cache Creek still attained maximum temperatures as high as 26°C. An exception to the above pattern was observed in the spring-fed Iron Springs Creek which maintained maximum water temperatures below 11°C for the second-order site and below 15°C for the third-order site during the postfire study years.

Water chemistry

Nitrate-nitrogen displayed over 20% more temporal change (measured as among-year CVs) in streams with burned catchments than in reference streams ($P < 0.11$), implying a strong influence of wildfire on instream nitrogen concentrations (Table 2). Robinson and Minshall (1996) found a direct relationship

Fig. 2. Historical (1938–1945) and postfire (1989–1992) discharge and precipitation values. Note the change in timing of peak discharge in the postfire years.

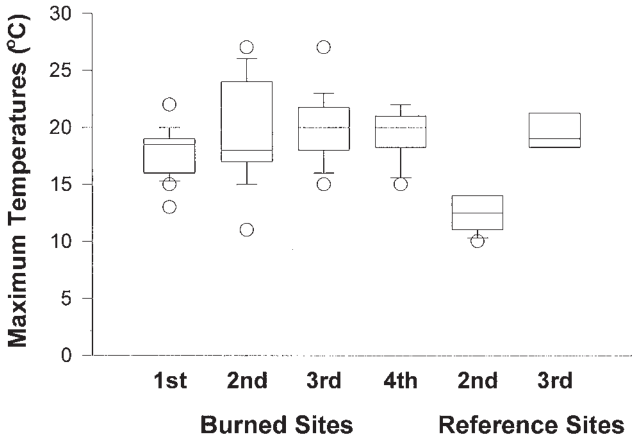


between loss of nitrogen and the percent catchment burned for these streams. Streams strongly influenced by extensive groundwater inputs (e.g., second-order Iron Springs) or that had highly confined channels due to geologic constraints (e.g., Lava Creek) typically had lower CVs for nitrate-nitrogen than other streams, regardless of the degree of catchment burned. Measures of ionic potential (i.e., pH, total hardness, total alkalinity, and specific conductance) exhibited similar and nonsignificant differences in mean CVs among stream groups ($P > 0.05$), indicating little temporal change in these constituents resulting from wildfire. Orthophosphorus had relatively high individual stream CVs; however, there were no significant differences in mean CVs among stream groups.

Woody debris

There was a substantial increase in the pieces of wood gained (attributed mostly to fire-felled trees) in most burned sites relative to reference streams (Fig. 4). Fewer pieces of woody debris were gained in larger (i.e., fourth order) than in smaller burned sites, with most of the increases in the number of wood pieces being observed in first- and significantly in third-order streams. For example, an average of 28 additional pieces of large woody debris per 50-m reach was recorded in third-order burned sites relative to only eight pieces gained in third-order reference streams in 1989 the first year following the wildfires. The source of wood in third- and fourth-order burned sites was equally partitioned between upstream (i.e., fire-felled trees) and riparian sources whereas wood in reference streams was primarily derived from the riparian zone (D.E. Lawrence, unpublished data). There was a significant loss of woody debris (>20 pieces/50 m) from burned sites in 1991 due to high discharge that was not evident in reference streams (<10 pieces/50 m)(Fig. 4). These data suggest that retention dynamics were altered (e.g., became less stable) in streams exposed to wildfire.

Fig. 3. Box plots of maximum water temperatures in different-sized burned and reference streams during the 5 years of study. Boxes represent means (central bar), standard deviations (box frame), 95% confidence limits (error bars), and outliers (circles) in maximum temperatures.



Channel morphology

The amount of channel cross-sectional area change over time was determined from the five permanent transects at each site and averaged by stream order. Relatively moderate change in channel morphology was observed for most burned sites between 1989 and 1990 (Fig. 5), probably due to below-normal

Table 2. Average among-year CVs for measured water chemistry variables for streams, with burned catchments grouped by size and reference streams.

Stream	Total hardness	Total alkalinity	Specific conductance	Field pH	Ortho-P	Nitrate-N
Burned catchments						
First-order sites						
Blacktail Deer, EF	5	13	17	1	24	60
Blacktail Deer, WF	16	18	23	2	35	81
Upper Cache	21	12	10	3	27	54
Fairy	16	24	10	2	29	55
Twin	17	21	29	6	37	72
Mean	15.0	17.5	17.8	2.6	30.3	64.4
SD	5.2	4.6	7.3	1.8	4.8	10.6
Second-order sites						
Lower Cache	9	8	17	1	29	47
Upper Cache	26	18	14	1	13	55
Fairy	16	16	17	2	32	74
Iron Springs	17	10	20	1	44	35
Blacktail Deer, Main	5	10	32	5	31	72
Mean	14.6	12.4	20.0	2.0	29.8	56.6
SD	7.2	3.9	6.3	1.5	9.9	14.8
Third-order sites						
Cache	8	14	14	4	38	55
Hellroaring	13	6	28	1	30	122
Iron Springs	21	12	13	1	24	55
South Cache	16	12	21	6	23	70
Lava	11	15	19	1	23	27
Mean	13.8	11.8	19.0	2.6	27.6	65.8
SD	4.4	3.1	5.4	2.1	5.8	31.4
Fourth-order sites						
Cache	12	27	12	6	35	59
Hellroaring	6	6	24	2	20	69
Lamar	11	7	19	4	31	83
Mean	9.7	13.3	18.3	4.0	28.7	70.3
SD	2.6	9.7	4.9	1.6	6.3	9.8
Reference streams						
Amphitheater	10	19	17	1	5	48
Rose	21	14	27	1	33	31
Pebble	10	20	18	1	29	50
Mean	13.7	17.7	20.7	1.0	22.3	42.9
SD	5.2	2.6	4.5	0.0	12.4	8.5

spring runoff in 1989 resulting from low snow accumulation during winter (e.g., see Ewing 1996). Most changes observed in channel profiles in 1989 were from first- through third-order sites with steep gradients. For example, channel depth increased in Twin Creek and the west fork (WF) of Blacktail Deer Creek between 1988 and 1989 whereas low-gradient Fairy and third-order Iron Springs creeks showed little change in channel morphology between 1988 and 1990 (Minshall and Robinson 1995). These differences among streams of similar order but different gradients caused the high variability in the summarized data of burned sites relative to reference streams (Fig. 5). Major runoff events during 1991 and 1992 resulted in most burned sites experiencing significant channel alterations that were not observed either previously or in similarly sized reference streams. For example, the channel of third-order Cache Creek widened and shifted laterally in 1991 and 1992 whereas reference sites displayed no change in channel morphology throughout the study period (Minshall and Robinson 1995).

Small burned streams showed the least, although still substantial, average amount of channel change among burned sites because of lithological constraints (Fig. 5). For example, the survey reach on upper Cache Creek was predominantly on bedrock, thus prohibiting additional channel downcutting following the initial disturbance, and Lava Creek (a burned site) also displayed minimal morphological change because of its highly confined channel. Regardless, high-gradient first- and second-order sites, e.g., Cache, WF and main Blacktail Deer, and Twin creeks, still displayed major changes in channel morphology in 1991 and 1992 (Minshall and Robinson 1995). Larger streams showed temporal patterns similar to smaller burned sites, with little channel change occurring in the low-gradient systems (e.g., third-order Iron Springs Creek) or in the reference Pebble Creek.

Fig. 4. Mean (+1 SD) number of pieces of wood gained or lost per 50 m counted in burned and reference streams by stream order from 1989 through 1992. Asterisks indicate sites that displayed significant differences ($P < 0.05$) among years.

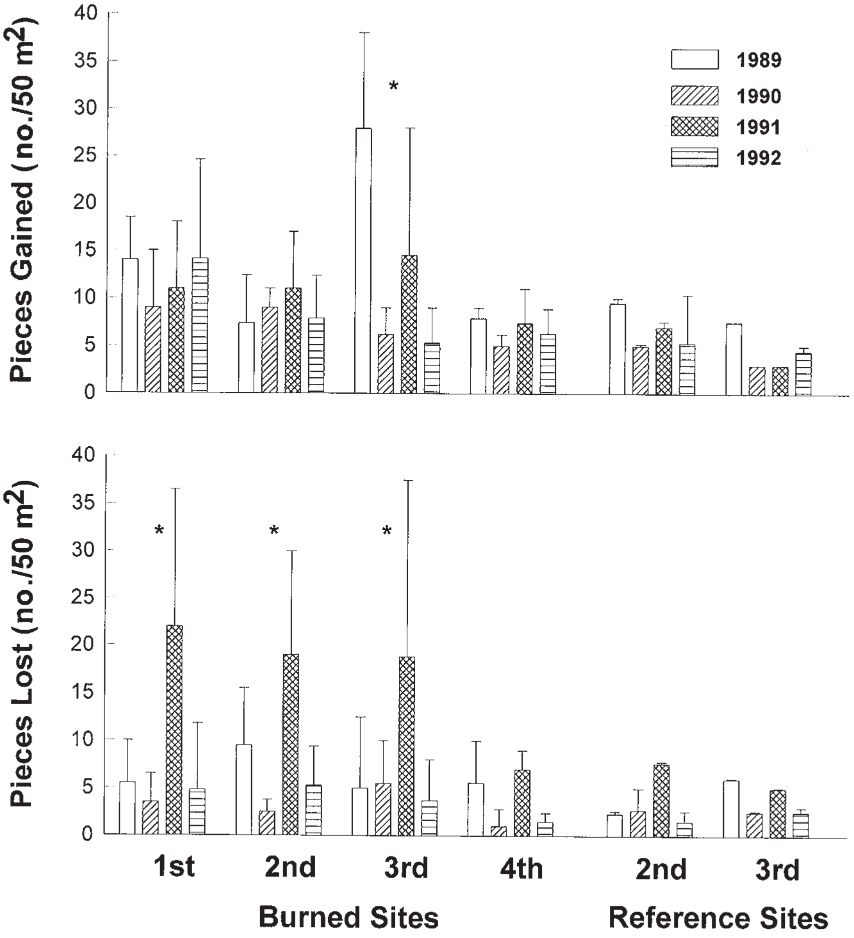


Fig. 5. Mean (+1 SD) change in channel area for burned and reference streams by stream order for October 1988 and August 1989–1992. Variation among individual burned sites is reflected in the large standard deviations. The asterisk indicates significant differences ($P < 0.05$) among years within the stream size.

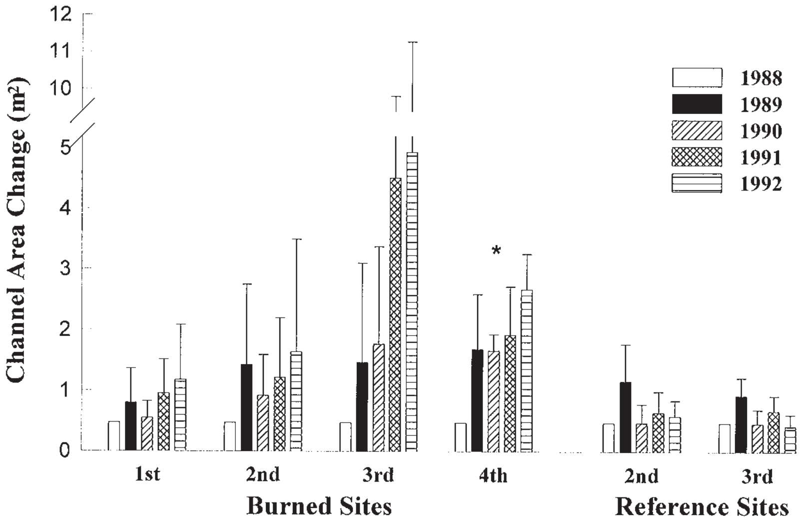
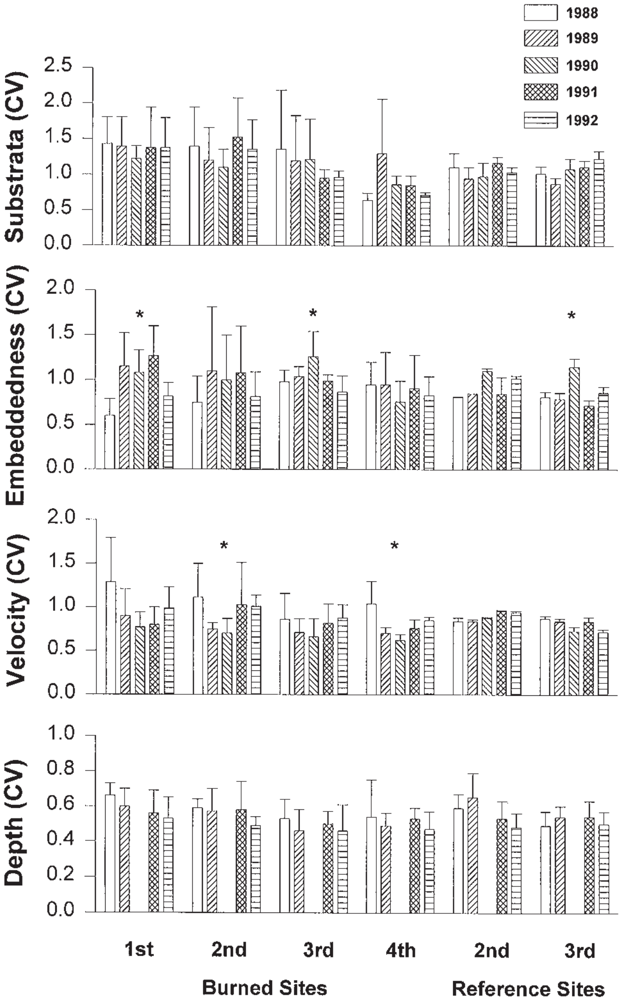


Fig. 6. Mean (+1 SD) annual CVs for stream substrata size, substrata embeddedness, near-bed water velocity, and water depth. See text for sample sizes and method of determination. Asterisks indicate sites with significant differences ($P < 0.05$) among years.



Instream habitat heterogeneity

Temporal changes in instream habitat conditions were assessed using CVs from the annual measures of substratum size and embeddedness, near-bed velocity, and water depth. There were no significant differences among substrata CVs over time for burned or reference streams (Fig. 6), suggesting little change in substrate heterogeneity resulting from the fires. In contrast, substrate embeddedness CVs significantly increased in first-order burned sites (with a similar trend in second-order sites) in postfire years 2–4, which was not seen in larger burned or reference streams. The differences in substrate embeddedness CVs in small burned sites indicate subtle changes in the amount and movement of fine sediments in these streams over time. For example, Minshall and Robinson (1995) suggested that a pulse of fine sediments had moved from smaller burned sites into larger streams during the first few postfire years. CVs for near-bed water velocity decreased in most burned sites after 1988 ($P < 0.10$), but were similar between years in reference streams ($P = 0.67$), indicating a reduction in the heterogeneity of near-bed water flow in the burned sites since the fire (Fig. 6). There were no significant differences among annual CVs for water depth in burned or reference streams.

Environmental conditions over time

To evaluate whether streams of burned catchments experienced any increased physical change over time relative to reference streams, we calculated among-year CVs for a number of important habitat variables and then summed these CVs for each study site (Table 3). The summed CVs were 100–200% higher in first- to third-order burned sites than in reference streams ($P < 0.001$) whereas fourth-order burned sites displayed values similar to those of reference sites ($P = 0.05$). Further, summed habitat CVs showed a strong positive regression against the percent of each catchment burned ($r^2 = 0.67$, $P = 0.05$), except for WF Blacktail Deer, inferring a strong physical response of stream ecosystems to wildfire. In addition, average summed CVs decreased as stream size increased, suggesting less influence of fire on the physical conditions of larger stream ecosystems. The exception, WF Blacktail Deer Creek, displayed low CVs for variables derived from changes in channel morphology.

Biological relationships

TOM and BOM

TOM, as CPOM or FPOM, generally increased in all burned sites and consisted primarily (>50%) of burned material (Fig. 7). High CPOM and FPOM levels after 1988 for burned sites relative to reference streams probably reflect increased overland input in burn catchments from increased runoff. The percent charcoal decreased and amorphous detritus increased in TOM in all burned sites after 1990 ($P < 0.05$), suggesting that much of the transported matter in 1990 was derived from new riparian growth or autotrophic production. However, the percent charcoal of TOM increased again in 1991 in burned sites, indicating substantial overland input of burned organic matter resulting from major runoff events during that year. The percent charcoal of TOM was always low in samples from reference streams.

The amount of benthic organic matter increased in most burned sites the first year following the fires and then decreased to reference levels by 1991 ($P < 0.05$) (Fig. 8). BOM levels were similar among years in respective fourth-order burn and reference sites ($P = 0.05$). About 20–40% of the benthic organic matter in burned sites was of burned material whereas the percent charcoal of BOM in reference sites remained below 20% throughout the study ($P < 0.01$). Mean periphyton standing crops (as chlorophyll *a* and AFDM) were greatest in October 1988 (two to five times) ($P = 0.05$), decreased in summer 1989, and then increased in subsequent summers in most burned and reference streams (Fig. 8).

Benthic macroinvertebrates

The average density of macroinvertebrates was substantially lower in third- and significantly lower in fourth-order burned sites in 1989 than in other years whereas no change occurred among years in reference streams ($P > 0.27$) (Fig. 9). The average biomass of macroinvertebrates increased, albeit nonsignificantly, from 1988 through 1990 and then decreased to 1988 levels by 1991 in burned sites; this trend also was not found in reference streams. There were no significant changes in mean

Table 3. CVs for physical measures recorded annually at each site during the 5-year study.

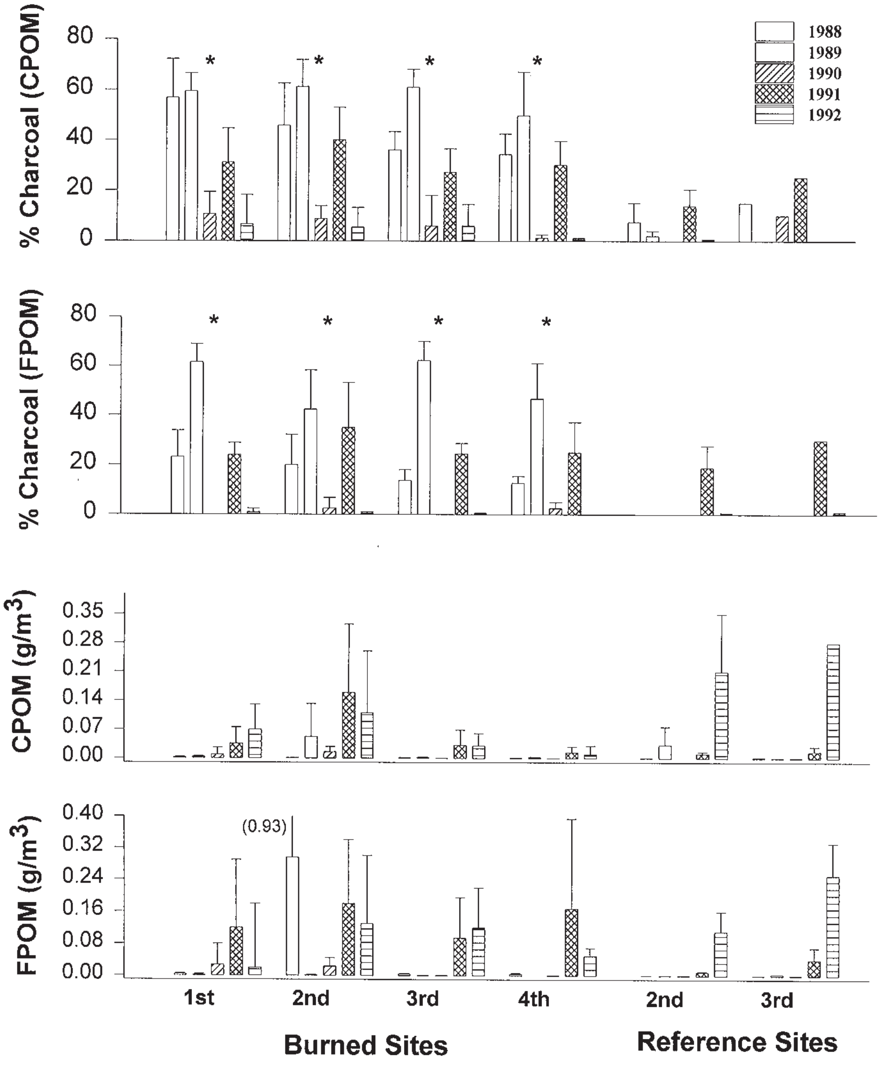
Stream	Order	Annual temperature range	Channel area change	Ratio channel area	Width/ depth ratio	Bank full channel width	% embeddedness	Bottom velocity	Water depth	Substrate size mean	Substrate size median	Summed CVs
Burned catchments												
First-order sites												
Blacktail Deer, EF	1	0.09	0.47	0.10	0.70	0.67	0.41	0.30	0.12	0.42	0.32	3.61
Blacktail Deer, WF	1	0.10	0.21	0.09	0.18	0.07	0.31	0.25	0.16	0.14	0.29	1.79
Upper Cache	1	0.06	0.62	0.03	0.64	0.49	0.32	0.38	0.34	0.27	0.49	3.64
Fairy	1	0.02	0.49	0.19	0.59	0.54	0.26	0.40	0.11	0.19	1.00	3.81
Twin	1	0.07	0.54	0.04	0.30	0.30	0.33	0.62	0.17	0.13	0.22	2.74
Mean		0.07	0.47	0.09	0.48	0.41	0.33	0.39	0.18	0.23	0.46	3.12
SD		0.03	0.15	0.06	0.23	0.23	0.05	0.14	0.09	0.12	0.32	0.85
Second-order sites												
Lower Cache	2	0.03	0.61	0.04	0.28	0.56	0.09	0.24	0.35	0.24	0.07	2.52
Upper Cache	2	0.17	0.69	0.03	0.59	0.56	0.19	0.29	0.07	0.15	0.50	3.24
Fairy	2	0.06	0.37	0.06	0.57	0.07	0.43	0.45	0.49	0.72	0.82	4.04
Iron Springs	2	0.21	0.36	0.19	0.41	0.20	0.28	0.29	0.31	0.87	0.24	3.35
Blacktail Deer, main	2	0.07	0.90	0.15	0.26	0.49	0.24	0.27	0.24	0.40	0.11	3.13
Mean		0.11	0.59	0.10	0.42	0.38	0.25	0.31	0.29	0.47	0.35	3.26
SD		0.08	0.23	0.07	0.15	0.23	0.12	0.08	0.15	0.31	0.31	0.54
Third-order sites												
Cache	3	0.09	0.77	0.09	0.23	0.12	0.21	0.94	0.11	0.28	0.37	3.21
Hellroaring	3	0.15	0.42	0.05	0.20	0.06	0.40	0.34	0.15	0.11	0.15	2.04
Iron Springs	3	0.15	0.30	0.16	0.27	0.30	0.22	0.52	0.08	0.47	0.21	2.68
South Cache	3	0.20	0.54	0.06	0.21	0.17	0.11	0.31	0.09	0.25	0.27	2.21
Lava	3	0.09	0.85	0.18	0.09	0.02	0.17	0.41	0.08	0.72	0.60	3.21
Mean		0.14	0.58	0.11	0.20	0.14	0.22	0.50	0.10	0.37	0.32	2.67
SD		0.04	0.23	0.06	0.07	0.11	0.11	0.26	0.03	0.24	0.18	0.55
Fourth-order sites												
Cache	4	0.13	0.48	0.03	0.30	0.03	0.26	0.22	0.21	0.10	0.28	2.05
Hellroaring	4	0.13	0.42	0.05	0.20	0.06	0.40	0.34	0.15	0.11	0.15	2.03
Lamar	4	0.07	0.49	0.01	0.08	0.03	0.19	0.37	0.07	0.13	0.30	1.75
Mean		0.11	0.46	0.03	0.19	0.04	0.28	0.31	0.14	0.11	0.24	1.94
SD		0.04	0.04	0.02	0.11	0.02	0.11	0.08	0.07	0.01	0.08	0.17
Reference streams												
Amphitheater	2	0.13	0.45	0.07	0.21	0.23	0.13	0.06	0.17	0.12	0.27	1.83
Rose	2	0.10	0.38	0.02	0.09	0.04	0.15	0.24	0.10	0.13	0.15	1.41
Pebble	3	0.09	0.32	0.03	0.15	0.02	0.21	0.22	0.14	0.20	0.32	1.70
Mean		0.10	0.38	0.04	0.15	0.10	0.16	0.17	0.14	0.15	0.25	1.65
SD		0.02	0.07	0.03	0.06	0.11	0.04	0.10	0.03	0.04	0.08	0.21

taxonomic richness or Ephemeroptera–Plecoptera–Trichoptera (EPT) taxonomic richness among sample years in burned or reference streams ($P > 0.05$) (Fig. 9). Minshall and Robinson (1995), however, documented a significantly reduced taxonomic richness (~10 taxa) in March 1989 (prior to the first spring snowmelt runoff after the fires) in some of the smaller burned sites that was not evident in larger burned sites or reference streams. This decrease in species richness suggests a more immediate effect of the fires on the macroinvertebrate communities in smaller streams, perhaps related to a reduced quality of food resources.

All burned sites showed major increases in the relative abundance of miners the first 2 years following the wildfires ($P < 0.10$) that were not evident in reference streams (Fig. 10). For example, miners constituted >50% of the assemblage in burned sites but <30% in reference streams in these years. Miner abundance decreased in burned sites to reference levels by 1991 (postfire year 3), being replaced with an increase in the relative abundance of gatherers ($P < 0.10$). In general, the abundance of scrapers was substantially less in first- and second-order burned sites than in third- and fourth-order burned and reference streams. In fact, scraper abundance actually increased in fourth-order burned sites during postfire years 2 and 3 ($P = 0.05$). Shredders increased in relative abundance only in the first-order burned sites in postfire years 3 and 4. The relative abundance of predators and filterers remained unchanged in burned and reference streams following the fires ($P > 0.05$).

Of the most abundant taxa, chironomids increased in postfire years 1 and 2 followed by a decrease in subsequent study

Fig. 7. Mean (+1 SD) TOM as CPOM or FPOM and percent charcoal of CPOM and FPOM from burned and reference streams by stream order from 1988 through 1992. See text for sample sizes. Asterisks indicate sites with significant differences ($P < 0.05$) among years.



years in all burned sites ($P = 0.05$) (Fig. 11). Indeed, chironomids constituted >40% of the assemblage in most burned sites but <30% in reference streams in the first two postfire years. *Baetis bicaudatus* increased in abundance, especially in third- ($P < 0.06$) and fourth-order ($P < 0.01$) sites, in burned sites each year following the fires and represented >20% of the macroinvertebrate assemblage in these streams by 1992. The abundances of chironomids ($P > 0.99$) and *Baetis* ($P > 0.59$) remained essentially unchanged among years in reference streams. The Oligochaeta displayed similar trends as *Baetis*. *Drunella doddsi* increased in abundance, constituting about 15% of the assemblage, in third- and fourth-order burned sites in postfire years 3 and 4 ($P = 0.05$).

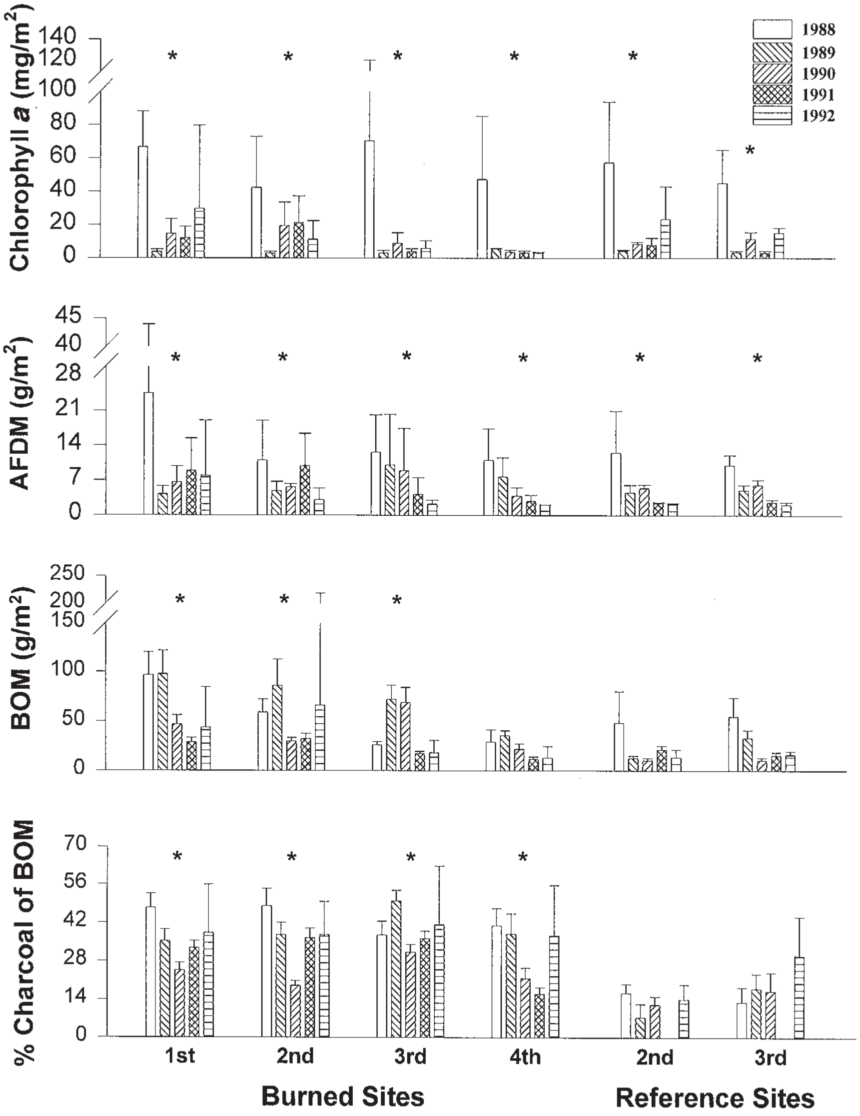
In contrast, *Cinygmula* abundance decreased over time in burned sites ($P < 0.05$) and displayed a similar trend in reference streams ($P < 0.02$) (Fig. 11). *Ephemerella infrequens* became more abundant, although nonsignificantly, in burned sites and also increased in relative abundance in the third-order reference stream. *Rhithrogena* densities were extremely reduced in first- and second-order burned sites relative to second-order reference streams, but increased in abundance to >14% of the assemblage in third- and fourth-order burned sites by postfire year 2 ($P < 0.05$). *Suwallia* abundance was greater in 1988 ($P = 0.05$) than in subsequent years in small burned sites; this was not observed in reference streams. *Zapada columbiana* maintained similar abundances among years in burned and reference streams ($P > 0.05$).

Discussion

Immediate effects

Our knowledge of the immediate effects of the Yellowstone fires is based on measurements and direct observations of the study streams and their catchments during the first several weeks following burning. Losses in catchment and riparian vegetation and almost instantaneous conversion of terrestrial vegetation to charcoal and ash were obvious and expected. These resulted in immediate changes in the amount of light and quality of materials, e.g., allochthonous food resources, entering the streams. Although most burned trees remained standing, many downed trees and large limbs were observed bridging and in streams. The most striking immediate

Fig. 8. Mean (+1 SD) periphyton chlorophyll *a* and AFDM, BOM, and percent charcoal of BOM for the burned and reference streams by stream order from 1988 through 1992. See text for sample sizes. Asterisks indicate sites with significant differences ($P < 0.05$) among years.

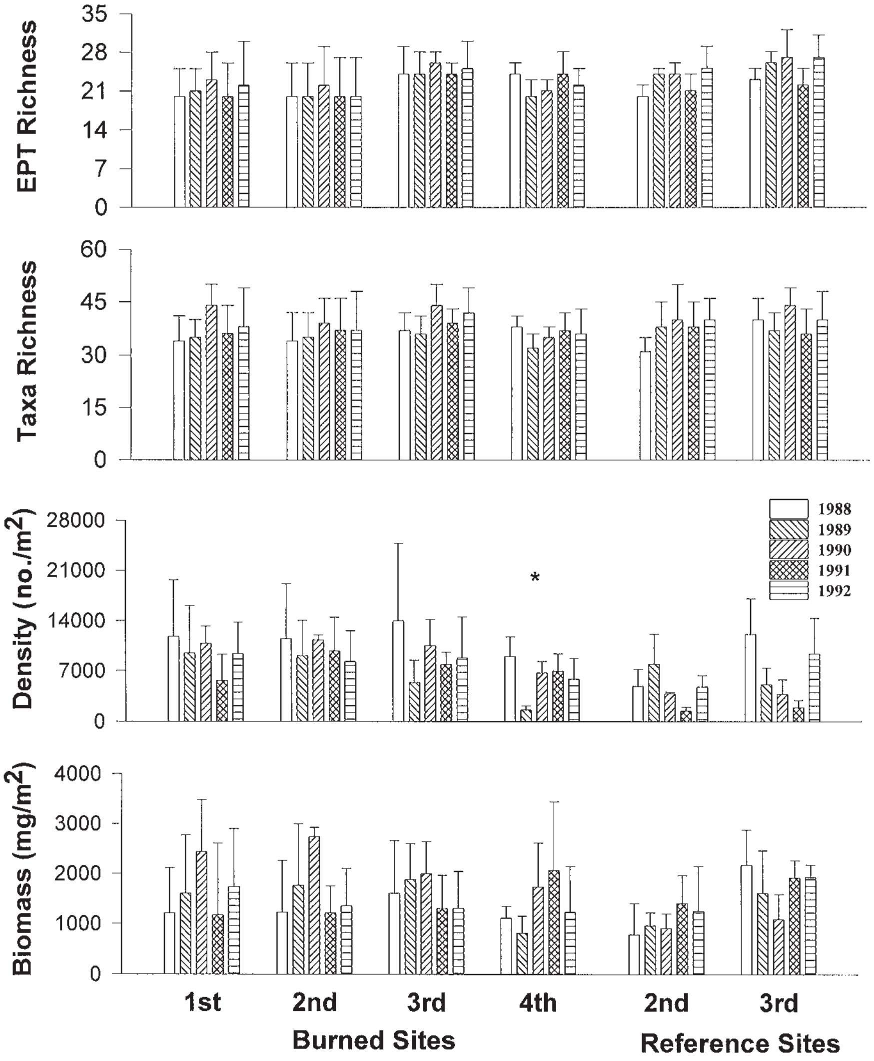


changes within the stream channel were the incineration and scorching of emergent mosses and heat fracturing (splaying) of rocks in and adjacent to first- and second-order streams. We also counted up to 10 dead cutthroat trout (*Oncorhynchus clarki*) per 250 m in third-order Cache and WF Blacktail Deer creeks.

Minshall et al. (1990) found that most dissolved chemical measures increased in streams of burned catchments the first year following the fires. Spencer and Hauer (1991) observed dramatic and rapid increases in phosphorus and nitrogen levels in streams during fire and attributed these increases to ash and to smoke gases, respectively. We suggest that high ammonia levels, highly soluble in gaseous form, arising from the smoke probably were responsible for the fish mortalities. Little or no immediate deleterious effect of fire was evident in periphyton standing crops or macroinvertebrate assemblages, even in the smallest streams observed (also see Albin 1979). These impacts are more difficult to discern due to the small size and rapid decay rates of the organisms involved. However, lotic macroinvertebrates are known to be adversely affected by exposure to ammonia (Gammeter and Frutiger 1990). Roby and Azuma (1995) showed that macroinvertebrate abundance and diversity were greatly reduced 3 weeks following wildfire in a northern California stream.

As hypothesized by Minshall et al.(1989), this study revealed distinct differences in the effects of wildfire on streams of different size. Following fire, headwater streams (first and second order) were more physically and chemically variable than intermediate-size burned streams (third and fourth order) or reference streams. In general, smaller streams had a greater proportion of their catchments burned than larger streams. For our study streams, the mean catchment burned was 75% for first- and second-order streams and 50% for third- and fourth-order streams. However, we also observed during aerial and ground reconnaissance that the catchments of many fire-impacted third- and fourth-order streams throughout Yellowstone Park and along its northern boundary with Montana were <50% burned and that this amount was much less for even

Fig. 9. Mean (+1 SD) macroinvertebrate EPT richness, taxa richness, density, and biomass in burned and reference streams by stream order from 1988 through 1992. See text for sample sizes. The asterisk indicates a site showing significant differences ($P < 0.05$) among years.



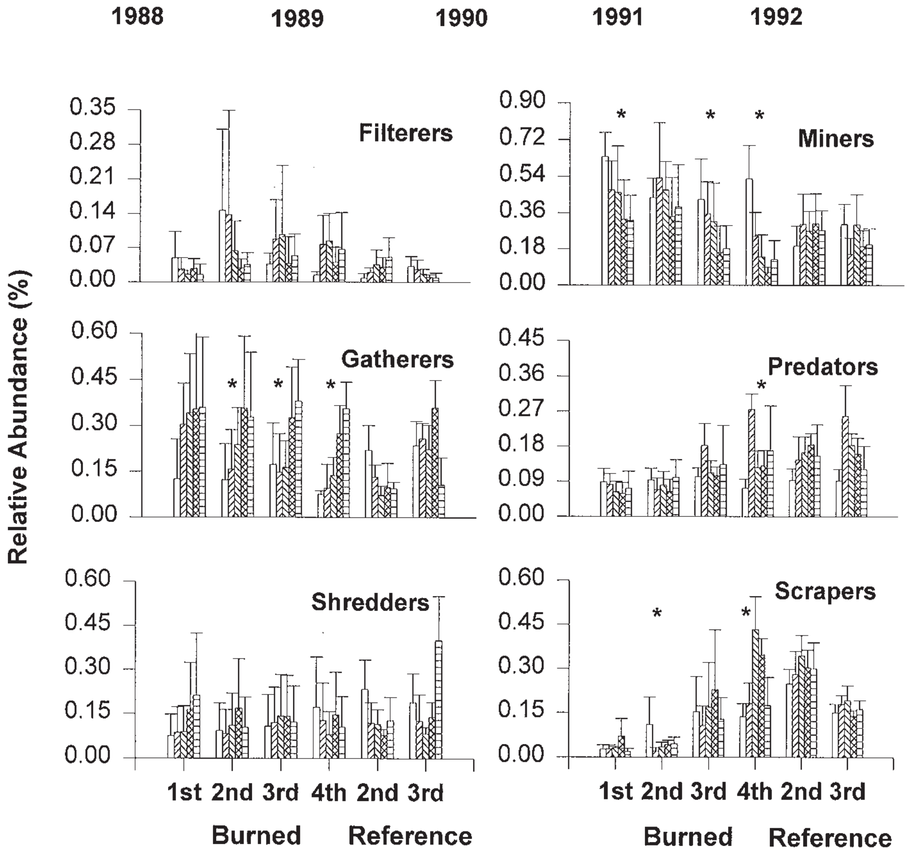
larger streams (no streams larger than sixth order are found in the park). As a result, the impact on biological properties also appeared more pronounced in smaller streams, although intermediate-size burned streams located in steep terrain with confined flood plains (e.g., third-order Cache and Hellroaring creeks) experienced greater amounts of overland flow and associated effects on the biota than other large study streams (Minshall and Robinson 1995).

The most consistent outliers from the general patterns found in this study were Fairy and Iron Springs creeks and were attributable to one or more relatively unique features. For example, besides being located in a different climate and underlain by different base rock (rhyolite) than other streams, (1) Fairy Creek sites had the lowest gradients of any study stream and the second-order site was unforested and strongly influenced by geothermal springs and (2) a large proportion of flow in Iron Springs Creek was groundwater; consequently, the third-order site displayed little variation in flow and usually did not freeze over in the winter.

Short-term effects

Minshall et al. (1989) showed that from October 1988 to March 1989, macroinvertebrate abundance, richness, and H' diversity decreased in six of eight monitored burned sites whereas these values increased or remained constant in the reference streams. Because no physical disturbances from runoff occurred during this period, we attribute these changes to high amounts of charcoal in stream benthos (>40%) and transport as a result of the fires. We further suggest that the input of charcoal decreased the palatability and quality (e.g., increased C:N values) of the organic matter pool as food. For example, Mihuc and Minshall (1995) found that only one taxon of 11 examined could utilize burned organic matter as a food source. Further, periphyton biomass decreased in burned streams (except third-order Iron Springs) during this period, although comparable changes were observed in reference streams. Data since 1989 indicate that burned organic matter is still being added to burned streams but in reduced amounts. Britton (1990) showed that BOM quantity and quality were altered the

Fig. 10. Mean (+1 SD) relative abundances of macroinvertebrate functional feeding groups (after Merritt and Cummins 1984) for burned and reference streams by stream order from 1988 through 1992. See text for sample sizes. Asterisks indicate sites showing significant differences ($P < 0.05$) among years.



first year following a prescribed burn but that the effect was short-term due to fast recovery by riparian vegetation. After 1990 (postfire year 2), most fire-related effects appear to be caused by physical disturbance of the stream bed associated with high runoff rather than changes in food resources.

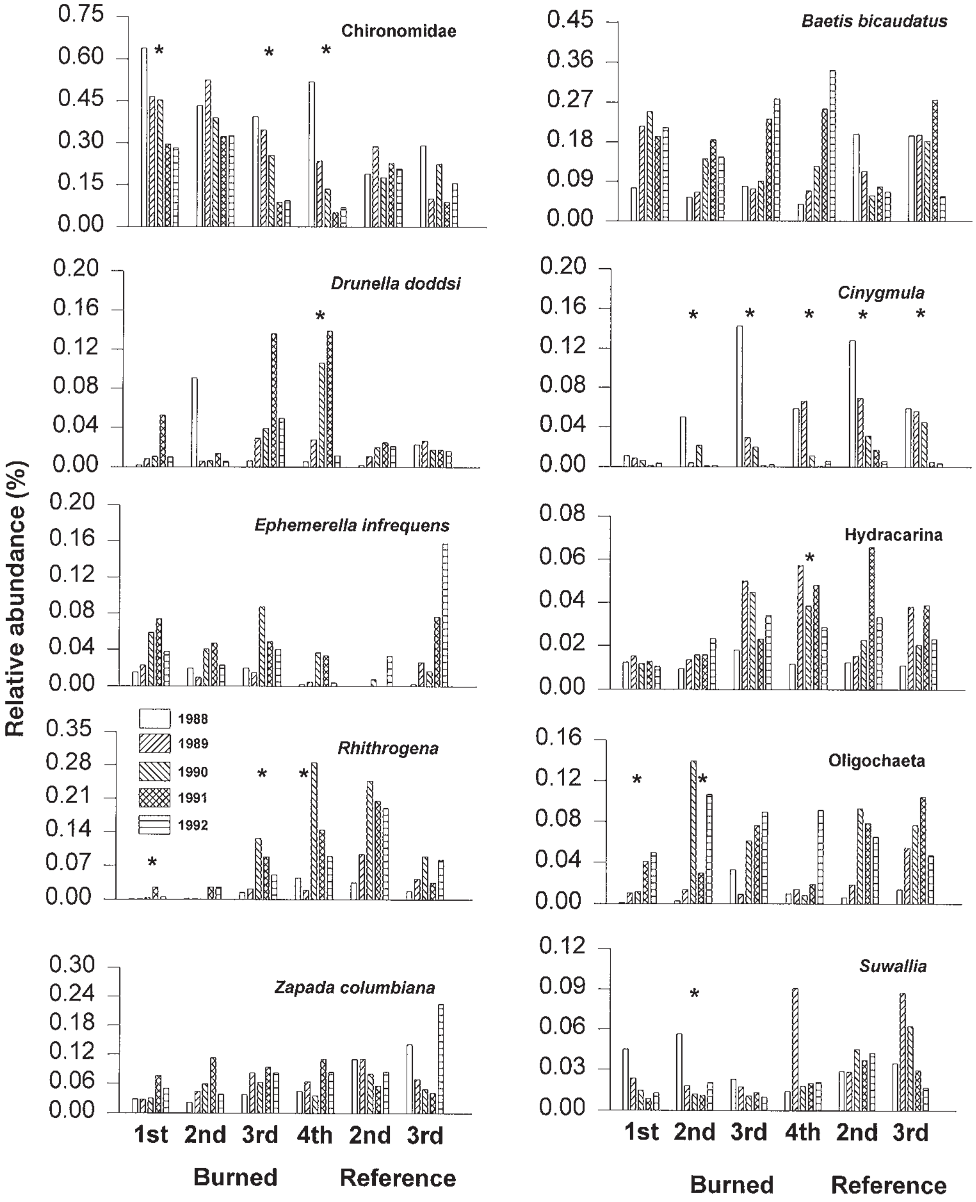
Spring melting of the 1989 snowpack was much slower than anticipated (P. Farnes, SCS, Bozeman, Mont., personal communication). Consequently, although several periods of “blackwater” associated with overland flow from heavy rains occurred between runoff and our August sampling, stream bed erosion and channel alterations were generally much less than expected or than occurred in later years. However, several first- through third-order streams, particularly Cache Creek and Hellroaring Creek catchments, did show substantial channel alteration and rearrangement of woody debris (Lawrence 1991). In addition, reductions in flow and substrate heterogeneity were observed in the burned streams, as indicated by changes in annual CVs in these measures, between 1988 and 1990. No comparable changes in either velocity or substratum occurred in our reference streams. A number of studies have documented similar changes in burned streams resulting from increased sediment loads and peaks in runoff (Tiedemann et al. 1979; Kusaka et al. 1983; Mitsudera et al. 1984; Helvey et al. 1985; Beaty 1994). Specifically, Beaty (1994) documented that median particle size initially decreased and then increased over time in a small stream following fire.

As documented in other studies, most dissolved constituents, especially nitrates, were higher in August 1989 than in October 1988, apparently in response to rainstorms during or immediately prior to the summer 1989 sample collections (also see Tiedemann et al. 1978; Nakane et al. 1983; Davis 1989; Britton 1991). In contrast with other ions (e.g., phosphorus, Spencer and Hauer 1991) that displayed only immediate changes in concentrations, temporal changes in instream nitrate levels typically reflected recovery by adjacent terrestrial vegetation (Bayley et al. 1992). Similarily, Robinson and Minshall (1996) found a direct correlation between nitrate loss and percent catchment burned in the Yellowstone study streams. Further, temporal changes in the quantity and quality of TOM and BOM between 1988 and 1989 suggest that charcoal and fine sediment were being transported from headwater streams and deposited downstream. Lastly, stream temperatures increased in smaller burn streams but remained unchanged in reference streams (also see Cushing and Olson 1963; Albin 1979).

Midterm effects

Although some major effects of fire were evident in the first three postfire years, burned streams appeared to be on a “fast recovery track” (sensu Minshall and Brock 1991). However, postfire year 3 (1991) was marked by at least two large runoff events that caused major physical changes in streams of burned watersheds with moderate to steep gradients. Ewing (1996) also noted that suspended sediment loads in the Lamar River

Fig. 11. Mean relative abundance of the 10 most common macroinvertebrate taxa collected in burned and reference streams by stream order from 1988 through 1992. Error bars deleted for clarity of presentation. See text for sample sizes. Asterisks indicate sites showing significant differences ($P < 0.05$) among years.



were much higher in 1991 and reflected the greater precipitation in this year. Additional channel modifications were observed in 1992, especially in the Cache Creek catchment. These disturbances were reflected in declines in biotic properties and served as important "resets" or delays in lotic ecosystem recovery (Minshall et al. 1989; Minshall and Brock 1991). Long-term studies are required to determine whether the frequency and magnitude of such disturbances will decrease over time as vegetation on the surrounding landscape recovers (sensu Minshall et al. 1989).

Our results show the importance of stream discharge and gradient in mediating physical disturbances associated with adverse intermediate effects (e.g., channel scouring and sediment loading) resulting from wildfire. High-gradient streams responded sooner (i.e., at lower flows) than low-gradient streams. For example, high-gradient tributaries showed major bed scouring and channel alteration the first two postfire years. At comparable discharges, high-gradient streams undergo greater physical disturbance than low-gradient streams. For instance, high-gradient burned streams displayed major changes (cutting or filling) in channel cross-section morphology in 1991 and 1992 whereas channel morphology of low-gradient burned streams and reference streams remained relatively constant.

Embeddedness data suggest that a pulse of fine sediments moved from burned watersheds into headwater streams and then gradually into larger burn streams over time. Median substrate size also decreased in first- through third-order burn streams following 1988 and remained low through 1992 (G.W. Minshall, unpublished data; also see Beaty 1994). An unexpected finding from our study was the maintenance of large amounts of fine inorganic sediments in headwater burn streams. From our study of streams in central Idaho (Minshall et al. 1990), we expected these materials to be rapidly removed and then increase again after 5–10 years. Because Yellowstone streams have lost a considerable amount of retentive capacity (Lawrence 1991; McIntyre and Minshall 1996) and periodically scour during high discharge, we believe that the "maintenance" of silt and sand is due to continued input from the surrounding catchment. This continued input also is suggested by the increase in percent charcoal of BOM in 1992. Comparable off-stream storage of fine materials apparently does not occur in the steeper, rockier central Idaho streams.

Woody debris in streams stabilizes stream channels (Nakamura and Swanson 1993), retains organic matter and sediment (Smith et al. 1993*a*, 1993*b*), and provides habitat important for fish and macroinvertebrates (Bilby and Likens 1980). First-through third-order streams contained the most wood and can be attributed to the lower competency of high flows to move larger pieces of wood and the closer proximity of trees to the main channel in smaller streams. In larger streams, high flows moved even the largest pieces of wood (including whole trees), leaving few pieces to stabilize the low-flow channel for more than a year. Small streams had lower debris volumes because a large proportion of fallen trees remained outside the channel margin. Bilby and Likens (1980) found an inverse relationship between stored organic matter and stream size, where first-order streams contained 75% and third-order streams held only 20% of the organic matter in the stream channel. Our data suggest that this relationship is altered in streams influenced by wildfire because of the reduced retention capacity in small burned streams (Lawrence 1991; McIntyre and Minshall 1996).

The effect of riparian zone burning was greatest in smaller streams and, as seen in this study, relatively fewer pieces of wood fell into the larger channels. Fallen wood in large streams is almost all drift or ramps (D.E. Lawrence, unpublished data), with few trees being tall and large enough to cross the entire channel. Wood in larger (third- and fourth-order) streams are found mostly outside the low-flow boundary because either a wood piece is outside the high-flow margin and thus stable or high flows deposit wood as drift onto braided gravel bars and high-flow point bars. Few pieces of wood are found in low-flow channels of larger streams, and thus, woody debris exerts little control on stream morphology. Robison and Beschta (1990) found increases in wood volume with increasing size of Alaskan streams, but they studied low-gradient streams where larger pieces of wood are stabilized for longer periods of time. In our study, large streams apparently are steep enough to move entire trees (75 cm diameter at breast height, >20 m long) having root wads.

Even 2 years following the 1988 fires, greater gross change in woody debris was present in burned than in reference streams due to an escalated gain in wood pieces. These newly fallen pieces are not secured and move more often than anchored wood. Bilby (1984) found that rearrangement of wood in streams of logged catchments was greater than in streams of unlogged catchments; a similar pattern was found in the present study with respect to fire. Associated with greater wood movement is the degree of channel scouring; disturbed streams experienced over 75 cm of scour in both studies. In contrast with logging impacts, we not only found an increase in woody debris loading immediately following catchment fire, but large snags will be available to enter the channel for about the next 20 years (Lyon 1984). Although significant rearrangement of woody debris in channels is still taking place, much woody debris is available to stabilize burn streams once side-slopes recover. For example, woody debris loads in burned sites were higher than in reference streams in 1992 (postfire year 4), but gains and losses of wood were comparable between the two stream types.

Preliminary predictions for stream habitat development can be made for streams in burned catchments based on our short- and mid-term results. Nearly all streams, especially second-order streams, are accruing pieces of wood. Keller and Tally (1979) found that between 50 and 100% of pool habitats in second- to fourth-order streams were formed by debris dams and more pools were debris related with increasing stream slope. As wood stabilizes, longer lasting pools are expected to form that will increase habitat for fish (Minshall et al. 1990; Nakamura and Swanson 1993). Because more wood was found in burned sites, we anticipate that more pools will form than in corresponding reference streams. In turn, an increase in adult fish density should accompany habitat development for up to 50 years following catchment fires. After that time, log decomposition and lack of large replacement trees may cause decreases in pool size and frequency and thus reduce fish habitat. Large trees will again enter stream channels forming deep pools and maximizing fish habitat around 150 years following fire, as found in Oregon streams (G. Reeves, U.S. Forest Service, Corvallis, Oreg., personal communication). However, habitat diversity decreased in Oregon streams of climax forests and this suggests that wildfire may play an integral role in creating more optimal habitat for fishes.

Macroinvertebrate communities in burned sites displayed major changes in response to the observed changes in the physical environments. For example, burned sites exhibited functional feeding group composition different from that in reference streams, suggesting alterations in food resources and a shift to more trophic generalists (e.g., Mihuc and Minshall 1995). However, the macroinvertebrate responses appeared to be more individualistic rather than associated with community properties. Community properties, such as species richness and diversity, showed substantial recovery within the first year following the wildfires whereas assemblage composition displayed significant changes that were apparent even in postfire year 5 (also see Richards and Minshall 1992). The changes wrought by fire affect macroinvertebrates in many more ways than just through alterations in food resources, e.g., via higher water temperatures. Individual life histories and lifestyles respond in different ways and to different degrees to these various changes. Opportunistic species, particularly those well suited for dispersal through drift and with relatively short generation times (such as chironomids and *Baetis*), seem to be especially adapted to conditions following fire, regardless of their trophic niche (Anderson 1992; Mihuc et al. 1996). In contrast, other species decreased in abundance soon after the fire and showed little or no recovery during this study. This was particularly noticeable among the Ephemeroptera, especially the dorsoventrally compressed taxa (e.g., *Cinygmula*, *Epeorus*, and *Rhithrogena*).

Our results emphasize the importance of studying stream ecosystems for a number of years following large-scale disturbance. Conclusions based on only one or a few years of data can be misleading in terms of overall trends, as evidenced, for example, by the apparent devastation of stream ecosystems immediately after the 1988 fires, their rapid progress toward recovery in postfire years 1 and 2, and their equally abrupt downturn in postfire years 3 and 4. Far too little data exist on conditions over extended periods after fire to know for certain whether the expectations for Yellowstone (Minshall et al. 1989; Minshall and Brock 1991) will prove correct. In fact, the initial recovery trajectory seen for Yellowstone streams is much different (faster initially, longer time delay before major storm impacts were seen, etc.) than expected based on the only other comparable study in central Idaho (Richards and Minshall 1992). The absence of comparable data on long-term effects, high year-to-year variability in postfire disturbance impacts among streams of different size, and differences in recovery trajectories compared with those found in other Rocky Mountain streams provide strong arguments for obtaining an extended temporal perspective for Yellowstone lotic ecosystems in the aftermath of the 1988 fires.

Acknowledgments

R.E. Gresswell and R.D. Jones of the U.S. Fish and Wildlife Service and J. Fowler and J.D. Varley of the National Park Service in Yellowstone National Park helped immeasurably with logistical matters related to this study. We thank George McKay and others for access to the GIS data and the provision of an academic internship for D.E. Lawrence. Numerous individuals helped to make the field work both successful and enjoyable: D.A. Andrews, M. Arunachalam, S.J. Bailey, C. Biastock, G.T. Boltzs, D.G. Carty, D. Chan, P.D. Dey, P. Koetsier, D.L. Mahony, M.J. McIntyre, S. McIntyre, T.B. Mihuc, J.M. Minshall, J.N. Minshall, S.C. Minshall, G.C. Mladenka, T. Mladenka, K. Moholt, D.C. Moser, C.A. Nelson, J.S. Nelson, B. Parker, S.E. Relyea, T.V. Royer, D. Taylor, R.L. Vannote, J. Wood, and G. Zappetti. Others who helped with sample collection are R. Ewing, J. Mohrman, and L. Wallace. In addition, many of the field personnel also helped with the processing of samples and (or) data in the laboratory where they were joined by S. Boyce, J. Check, T.N. Curzon, R. Gill, J. Mihuc, H.M. Nelson, B.E. Olenick, M.A. Overfield, L.M. Reed, K.W. Sant, and S.A. Thomas. P. Farnes and J. Mohrman generously provided data and information on precipitation and runoff. Gill Deans, Kevin Calloway, and Jake Clark provided various levels of horsepacking skills from novice to expert. The "bear brothers," M. Harrelton and J. Jonkel, shared their cabin, grub, and tall tales with us on Hellroaring Creek in 1988. We gratefully thank K.W. Cummins and family for accommodations at Cooke City, Mont. This project was funded by grants from the National Science Foundation (BSR-17819) and the University of Wyoming/National Park Service Research Center. In addition, the National Park Service and U.S. Fish and Wildlife Service in Yellowstone contributed helicopter flights, lodging, horses, and personnel to aid with field work. We appreciate the comments of K. Lohman and two anonymous reviewers that improved the manuscript.

References

Albin, D.P. 1979. Fire and stream ecology in some Yellowstone Lake tributaries. Calif. Fish Game, **65**: 216–238.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation (APHA). 1989. Standard methods for the examination of water and wastewater. APHA, New York.

Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. Hydrobiologia, **248**: 71–92.

Bayley, S.E., Schindler, D.W., Beaty, K.G., Parker, B.R., and Stainton, M.P. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Can. J. Fish. Aquat. Sci. **49**: 584–596.

Beaty, K.G. 1994. Sediment transport in a small stream following two successive forest fires. Can. J. Fish. Aquat. Sci. **51**: 2723–2733.

Bilby, R.E. 1984. Post-logging removal of woody debris may affect stream channel stability. J. For. **82**: 609–613.

Bilby, R.E., and Likens, G.E. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology, **61**: 1107–1113.

Bovee, K.D., and Milhous, R. 1978. Hydraulic simulation in instream flow studies: theory and techniques. Cooperative Instream Flow Service Group, Western Energy and Land Use Team, U.S. Fish and Wildlife Service, Fort Collins, Co.

Britton, D.L. 1990. Fire and the dynamics of allochthonous detritus in a South African mountain stream. Freshwater Biol. **24**: 347–360.

Britton, D.L. 1991. Fire and the chemistry of a South African mountain stream. Hydrobiologia, **218**: 177–192.

Cushing, C.E., and Olson, P.A. 1963. Effects of weed burning on stream conditions. Trans. Am. Fish. Soc. **92**: 303–305.

Davis, E.A. 1989. Prescribed fire in Arizona chaparral: effects on stream water quality. For. Ecol. Manage. **26**: 189–206.

Despain, D.G. 1987. The two climates of Yellowstone National Park. Proc. Mont. Acad. Sci. **47**: 11–19.

Ewing, R. 1996. Postfire suspended sediment from Yellowstone National Park, Wyoming. Water Resour. Bull. **32**: 605–627.

Gammeter, S., and Frutiger, A. 1990. Short-term toxicity of NH_3 and low oxygen to benthic macroinvertebrates or running waters and conclusions for wet weather water pollution control measures. Water Sci. Technol. **22**: 291–296.

Greeson, P.E., Ehlke, T.A., Irwin, G.A., Lium, B.W., and Slack, K.V. (*Editors*). 1977. Methods for collection and analysis of aquatic biological and microbiological samples. Techniques of Water Resources Investigations, U.S. Geologic Survey. U.S. Goverment Printing Office, Washington, D.C.

Helvey, J.D., Tiedemann, A.R., and Anderson., T.D. 1985. Plant nutrient losses by soil erosion and mass movement after wildfire. J. Soil Water Conserv. **40**: 168–173.

Kay, J.K. 1991. A nonequilibrium thermodynamic framework for discussing ecosystem integrity. Environ. Manage. **15**: 483–495.

Keller, E.A., and Tally, T. 1979. Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment. *In* Adjustments of the fluvial system. *Edited by* D. Rhodes and G.P. Williams. Kendall/Hunt Publishing Co., Dubuque, Iowa. pp. 132–142.

Knight, D.H., and Wallace, L.L. 1989. The Yellowstone fires: issues in landscape ecology. BioScience, **39**: 700–706.

Kusaka, S., Nakane, K., and Mitsudera, M. 1983. Effect of fire on water and major nutrient budgets in forest ecosystems: I. Water balance. Jpn. J. Ecol. **33**: 323–332.

Lawrence, D.E. 1991. Postfire woody debris dynamics in headwater streams of Yellowstone National Park. Master of Science thesis, Department of Biological Sciences, Idaho State University, Pocatello, Idaho.

Leopold, L.B. 1970. An improved method for size distribution of stream bed gravel. Water Resour. Res. **6**: 1357–1366.

Lind, O.T. 1979. Handbook of common methods in limnology. 2nd ed. C.V. Mosby Co., St. Louis, Mo.

Lorenzen, C.J. 1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res. **13**: 223–227.

Lyon, L.J. 1984. The sleeping child burn — 21 years of postfire change. U.S. For. Serv. Res. Pap. INT-330.

McIntyre, M.J., and Minshall,.G.W. 1996. Changes in transport and retention of coarse particulate organic matter in streams. *In* The ecological implications of fire in Greater Yellowstone, 1996. Proceedings second biennial conference on Greater Yellowstone Ecosystem. *Edited by* J.M. Greenlee. International Association Wildland Fire, Fairfield, Washington. pp. 59–75.

Merritt, R.W., and Cummins, K.W. 1984. An introduction to the aquatic insects. 2nd ed. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Mihuc, T.B., and Minshall, G.W. 1995. Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. Ecology, **76**: 2361–2372.

Mihuc, T.B., Minshall, G.W., and Robinson, C.T. 1996. Responses of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. *In* The ecological implications of fire in Greater Yellowstone, 1996. Proceedings second biennial conference on Greater Yellowstone Ecosystem. *Edited by* J.M. Greenlee. International Association Wildland Fire, Fairfield, Washington. pp. 83–94.

Minshall, G.W., and Brock, J.T. 1991. Anticipated effects of forest fire on Yellowstone stream ecosystems. *In* Greater Yellowstone's future: man and nature in conflict? *Edited by* B. Keiter and M.S. Boyce. Yale University Press, New Haven, Conn. pp. 123–135.

Minshall, G.W., and Robinson, C.T. 1995. Response of stream ecosystems to wildfire: Yellowstone National Park 1988–1993. Final Report to U.S. National Park Service. Yellowstone National Park, Wyoming.

Minshall, G.W., Brock, J.T., and Varley, J.D. 1989. Wildfires and Yellowstone's stream ecosystems: a temporal perspective shows that aquatic recovery parallels forest succession. BioScience, **39**: 707–715.

Minshall, G.W., Andrews, D.A., Brock, J.T., Robinson, C.T., and Lawrence, D.E. 1990. Changes in wild trout habitat following forest fire. *In* Wild Trout IV: Proceedings of the Symposium. *Edited by* F. Richardson and R.H. Hamre. U.S. Government Printing Office 774-173/25037, Washington, D.C. pp. 111–119.

Minshall, G.W., Robinson, C.T., Royer, T.V., and Rushforth, S.R. 1995. Benthic community structure in two adjacent streams in Yellowstone National Park five years after the 1988 wildfires. Great Basin Nat. **55**: 193–200.

Mitsudera, M., Kamata, Y., and Nakane, K. 1984. Effect of fire on water and major nutrient budgets in forest ecosystems: III. Rainfall interception by forest canopy. Jpn. J. Ecol. **34**: 15–25.

Molles, M.C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology, **63**: 1–6.

Nakamura, F., and Swanson, F.J. 1993. Effects of coarse woody debris on morphology and ediment storage of a mountain stream system in Western Oregon. Earth Surf. Processes Landforms, **18**: 43–61.

Nakane, K., Kusaka, S., Mitsudera, M., and Tsubota, H. 1983. Effect of fire on water and major nutrient budgets in forest ecosystems: II. Nutrient balances, input (precipitation) and ouput (discharge). Jpn. J. Ecol. **33**: 333–345.

Platts, W.S., Megahan,W.F., and Minshall, G.W. 1983. Methods for evaluating stream, riparian, and biotic conditions.U.S. For. Serv. Gen. Tech. Rep. INT-138.

Reice, S.R., Wissmar, R.C., and Naiman, R.J. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environ. Manage. **4**: 647–659.

Resh, V.H., Brown, A.V, Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and Wissmar, R. 1988. The role of disturbance theory in stream ecology. J. North Am. Benthol. Soc. **7**: 433–455.

Richards, C., and Minshall, G.W. 1992. Spatial and temporal trends in stream macroinvertebrate communities: the influence of catchment disturbance. Hydrobiologia, **241**: 173–184.

Robinson, C.T., and Minshall, G.W. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. J. North Am. Benthol. Soc. **5**: 237–248.

Robinson, C.T., and Minshall, G.W. 1996. Physical and chemical responses of streams in Yellowstone National Park following the 1988 wildfires. *In* The ecological implications of fire in Greater Yellowstone, 1996. Proceedings second biennial conference on Greater Yellowstone Ecosystem. *Edited by* J.M. Greenlee. International Association Wildland Fire, Fairfield, Washington. pp. 217–221.

Robinson, C.T., Rushforth, S.R., and Minshall, G.W. 1994. Diatom assemblages of streams influenced by wildfire. J. Phycol. **30**: 209–216.

Robison, E.G., and Beschta, R.L. 1990. Characteristics of coarse woody debris for several coastal streams of southeast Alaska, USA. Can. J. Fish. Aquat. Sci. **47**: 1684–1693.

Roby, K.B., and Azuma, D.L. 1995. Changes in a reach of a Northern California stream following wildfire. Environ. Manage. **19**: 591–600.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. **52**: 199–221.

Romme, W.H., and Despain, D.G. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience, **39**: 695–699.

Smith, R.D., Sidle, R.C., and Porter, P.E. 1993*a*. Effects of bedload transport of experimental removal of woody debris from a forest gravel-bed stream. Earth Surf. Processes Landforms, **18**: 455–468.

Smith, R.D., Sidle, R.C., Porter, P.E., and Noel, J.R. 1993*b*. Effects of experimental removal of woody debris on the channel morphology of a forest, gravel-bed stream. J. Hydrol. **152**: 153–178.

Spencer, C.N., and Hauer, F.R. 1991. Phosphorus and nitrogen dynamics in streams during wildfire. J. North Am. Benthol. Soc. **10**: 24–30.

Stockner, J.G., and Armstrong, F.A.J. 1971. Periphyton of the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28**: 215–229.

Talling, J.R. 1973. The application of some electrochemical methods to the measurement of photosynthesis and respiration in fresh waters. Freshwater Biol. **3**: 335–362.

Tiedemann, A.R., Helvey, J.D., and Anderson, T.D. 1978. Stream chemistry and watershed nutrient economy following wildfire and fertilization in Eastern Washington. J. Environ. Qual. **7**: 580–588.

Tiedemann, A.R., Conrad, C.E., Dieterich, J.H., Hornbeck, J.W., Megahan, W.F., Viereck, L., and Wade, D.D. 1979. Effects of fire on water. USDA For. Serv. Gen. Tech. Rep. WO-10.

Weber, C.I. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. EPA-670/4-73-001, U.S. Environmental Protection Agency, Cincinnati, Ohio.

White, P.S., and Pickett, S.T.A. 1985. Natural disturbance and patch dynamics: an introduction. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P.S. White. Academic Press Inc., Orlando, Fla. pp. 3–13.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.