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FUNCTIONAL CHARACTERISTICS OF WILDERNESS STREAMS TWENTY YEARS FOLLOWING WILDFIRE

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ABSTRACT.—We compared functional attributes of streams draining catchments burned by wildfire 20 years previously to those of streams in unburned catchments. Long-term analyses of channel profiles indicated most channel change occurred within the first 10 years after fire with little subsequent change the following 10 years. Much of the standing dead timber had fallen, and its effect on stream morphology was directly related to stream size, with important ramifications for future years as decay progresses. The volume of wood in the active channel was 5X higher in a 3rd-order burn stream than in other burn or reference streams, but >80% of this wood was still bridging the stream. Retention of leaves was strongly associated with channel morphology and location of debris dams. Sediment respiration was significantly greater (1.7X) in streams of burned catchments, resulting from greater amounts of loosely attached organic matter in the sediments of these streams. In concordance with respiration results, coefficients of exchange (k_{ex}) were almost 5X higher in burn streams than in reference streams, although estimates of transient storage were similar between stream types. We expect the input of large woody debris to increase in the next 10 years in fire-impacted streams as bridging trees collapse into the stream, thereby enhancing channel complexity and habitat heterogeneity, instream metabolism and retention, and consequently stream function. The results emphasize the importance of landscape history, such as large-scale wildfires, on present patterns and processes in stream ecosystems.

Key words: retention, uptake, woody debris, metabolism, storage, channel morphology.

Landscape history profoundly influences ecological patterns and processes of lotic ecosystems today. For example, past glacial events have directly affected current distributions of many freshwater organisms such as fish (Hershey et al. 1999) and macroinvertebrates (Sweeney et al. 1992). In a more recent context, historical land use patterns by humans have direct consequences on the present diversity of stream macroinvertebrates (Harding et al. 1998). These historical "habitat filters" (sensu Tonn 1990) shape biotic assemblages and provide a mechanistic understanding of the response of these assemblages to disturbance (e.g., Poff 1997). Consequently, a historical context is required to more fully appreciate and even elucidate habitat constraints (spatial and temporal) on the structure and function of lotic ecosystems. History is an important but little appreciated component of habitat templet theory (sensu Southwood 1977).

Large-scale disturbances are infrequent and can vary substantially in their spatial extent and temporal intensity (Foster et al. 1998). For instance, wildfire can produce abiotic and biotic legacies that influence ecosystem structure and function for decades to centuries. These legacies (biotic remnants) have direct bearing, for example, on successional patterns and overall recovery of ecosystems following disturbance (Turner et al. 1998). Because large disturbances are infrequent and ecosystem changes following large disturbances are long-term (Minshall and Brock 1991), few studies have documented recovery processes over the decades following large disturbances, particularly in stream ecosystems. Indeed, Gresswell (1999) argues that the temporal response of lotic ecosystems to wildfire has been essentially ignored.

Wildfire is a landscape-level disturbance that has profound long-term effects on ecosystem response and recovery. Wildfires vary in extent and intensity, and this variability has important abiotic and biotic consequences for streams and rivers in burned catchments (Minshall et al. 1997). Because of the tight coupling between streams and the terrestrial landscape through which they flow (Hynes 1975), the recovery of streams following wildfire can be partitioned into temporal components that

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reflect successional changes in the regrowth of terrestrial vegetation and decomposition characteristics of burned terrestrial organic matter (Minshall and Brock 1991). Minshall et al. (2004) categorized these stages in stream response and recovery as (1) immediate changes (the time of active burning to a few days after); (2) short-term changes (a few days to the beginning of spring runoff); (3) mid-term changes (from spring runoff of the 1st postfire year to sometime beyond the 10th year); and (4) long-term changes (occurring decades or centuries later).

An important terrestrial component that directly affects stream systems in burned catchments is the relatively rapid recovery of riparian vegetation and the falling of most standing dead timber within the first 5–20 years (Minshall et al. 1990). The falling of dead trees has important intermediate to long-term consequences in the retention, stability, and function of streams that are expected to be in direct contrast to the immediate and short-term responses (e.g., lower channel stability and retention) of these systems to wildfire. Readers are referred to Minshall et al. (2001a, 2001b) for data regarding various short-term (1st year) and mid-term (years 1–10) responses of streams following wildfire. The goal of the present study was to compare functional attributes (e.g., ecosystem metabolism) of streams in catchments burned 20 years previously relative to reference streams in unburned catchments.

STUDY SITE DESCRIPTION

The study was conducted in late July 1999 on 6 streams in the remote Frank Church River of No Return Wilderness in central Idaho, USA. The area is roadless, being accessible only by trail or via occasional airfields by light aircraft. Elevations range from about 1200 m to 3150 m a.s.l., with valley side-slopes averaging 45%–70%. The geology of the area is underlain by Challis Volcanics (rhyolitic to andesitic rock) intruded by Idaho Batholith (Ross 1934); some river valleys also contain Quaternary glacial deposits. Soils are loamy sand to sandy loam (Cater et al. 1973) and poorly developed. Precipitation, mostly as snow, ranges from 38–50 cm in the valleys to 76–100 cm at higher elevations. The area is lightly to moderately forested, with subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) found predominantly at higher elevations, Douglas-fir (*Pseudotsuga menziesii*) at mid-elevations, and ponderosa pine (*Pinus ponderosa*) mostly at lower elevations. Sagebrush (*Artemisia*) and grasses are common at mid- and low elevations, particularly on south-facing slopes. Riparian vegetation includes alder (*Alnus*), aspen (*Populus tremuloides*), water birch (*Betula occidentalis*), cottonwood (*Populus*), and willow (*Salix*). Minshall et al. (2001a, 2001b) provide additional details of the study area.

All study streams are tributaries of the Middle Fork Salmon River, with 3 of them having a significant part of their catchment (54%–81%) burned by wildfire (Mortar Creek fire) in 1979 (Table 1). The other 3 streams were unburned by the Mortar Creek fire but experienced less extensive wildfires in their respective catchments during the 20 years following 1979, especially in 1988 (Minshall et al. 2001b). The streams are located within 15 km of each other at elevations between 1329 m and 1414 m a.s.l. and range in size from 2nd to 5th order. Drainage aspect is primarily southern for burned catchments and northern for unburned catchments. Stream slopes are 6%–11% for the smaller streams and 2%–4% for the larger study streams. Maximum water temperatures in summer were 12° to 17°C. Stream water pH (daytime) ranged from 8.3 to 8.6, alkalinity from 38 to 102 mg · L^{-1} $CaCO_3$, and specific conductance between 50 and 120 μs · cm^{-1}.

METHODS

Physical attributes of the streams were characterized using measures of substrate size and embeddedness, water depth, and bankfull width (as defined in Davis et al. 2001). We determined substrate size (mid-axis) and percent embeddedness (quartile percent) by measuring 100 randomly selected rocks along a 100-m length of stream. Study reaches were selected in 1979, the initial year of study, to represent relative conditions along each stream. We visually estimated embeddedness as the degree of interstitial filling of the substratum by fine inorganic particles (after Minshall et al. 1997). Water depth also was recorded at these 100 locations. Bankfull widths were recorded at 5 transects 25 m equidistant from each other, with the 1st transect being the initial permanent transect determined in 1979 (Minshall et

TABLE 1. Catchment characteristics of study sites. Area burned refers to percent of the catchment that was burned by wildfire in 1979: B = burned catchment and U = unburned catchment.

Stream	Area burned (%)	Stream order	Link	Elevation (m)	Area (km^2)	Channel slope (5)	Drainage aspect	Specific conductance at 25°C
Little (B)	81	2	7	1408	5.1	6	S	138
Pungo (U)	trace	2	10	1396	13.8	7	NE	112
WF L Loon (B)	54	3	24	1341	20.7	4	SW	100
EF Indian (U)	trace	3	12	1413	17.3	3	NE	111
EF L Loon (B)	61	5	105	1329	84.0	2	S	117
Indian (U)	trace	5	89	1414	212.7	1.5	NW	78

al. 2001a, 2001b). Subsequent transects were placed upstream of the 1st one. Channel cross sections were recorded each year at the permanent transect established in 1979. For the purpose of this paper, channel profiles for 3 years (1980, 1988, and 1999) are presented in the results for the study streams. Streams were characterized chemically in the field using portable pH and specific conductance meters (Orion Corp., USA). We recorded diel water temperatures for each stream using temperature loggers (Vemco minilogs) during the time of sampling, usually 1–2 days. Sample days were sunny and represented typical summer temperatures for each study stream.

The volume of large (>5 cm diameter) woody debris was recorded within a 50- to 100-m reach in each stream beginning immediately upstream of the 1st transect used for determining bankfull width. Each piece of large woody debris within the bankfull width was measured (diameter and length) and categorized as either bridging the stream or having potential for enhancing stream retention. Conglomerates of woody debris, i.e., debris masses retained by larger pieces of woody debris, also were measured for total volume. Volume was determined based on respective geometric shapes of the measured debris.

Because of time constraints in the field, e.g., 3–6 hours per stream, we could determine leaf retention at only 4 of the study streams (Little, EF Indian, Pungo, and WF Little Loon Creeks). At each site we collected 300–400 fresh alder leaves from trees in the riparian zone. Essentially no fresh leaves were observed in any of the study reaches prior to release of the treatment leaves. Collected leaves were transported to the most upstream transect and individually released over a period of about 3 minutes. After 1 hour we collected leaves from the stream channel beginning 50 m downstream of the release point and proceeding upstream, summing for each 5-m increment. Each 50-m reach was examined for leaves twice. The predominant habitat type of each 5-m segment within the 50-m reach was scored as pool, run, or riffle, and also for presence of debris dams.

Sediment metabolism was quantified in each stream using an in situ oxygen-depletion method (after Jones et al. 1995). Fine sediment (<8 mm diameter) was collected by shovel from the stream bottom after removal of surface sediment (typically 10–15 cm in depth) and placed into clear plexiglass tubes (5 cm wide × 30 cm long, volume = 0.6 l, n = 3 per stream). Half of each tube was filled with sediment and the remaining space with stream water. Water oxygen concentrations were measured (WTW Oxi 340, Weilheim, Germany) and the tube capped off with a rubber stopper. The rubber stopper had a vent that allowed all air trapped in the tube to be released; thus, the tube was filled only with stream sediment and ambient stream water. Once the tubes were sealed, they were buried in the stream to eliminate effects of solar radiation on metabolism. The tubes were allowed to incubate for a period of 3–4 hours, retrieved, and the oxygen concentration remeasured. Tubes were incubated in the stream beginning in late morning around 1030–1100. For comparison among sites, sediment respiration rates were normalized to 20°C using an Arrhenius temperature coefficient of 1.072. The contents from each tube were stored in plastic zip-type bags and kept in the dark for transport to the laboratory.

In the laboratory the organic content of the sediments was determined. First, loosely attached particulate organic matter (LPOM) was elutriated, split into size fractions <63 and >63 μm, and determined as ash-free dry mass (AFDM). These sediments were dried at 60°C for at least 4 days, weighed, ashed at

500°C for 4 hours, and reweighed. The difference in weights was an estimate of the AFDM. In addition, the remaining organic matter that was attached to the sediments also was measured as AFDM. ANOVA was used to test for significant differences in the measured variables between streams of burned and unburned catchments (Zar 1984).

We estimated transient water storage using a pulse release of a conservative tracer (NaCl) and recording changes in specific conductance of the stream water at 2 locations downstream of the release point as the pulse of tracer moved through the system. The 1st location was immediately downstream of the effective mixing zone, the 2nd location about 100 m downstream of the first. The transient storage zone (A_t as m^2) and coefficient of exchange (k_{ex} as $m^2 \cdot s^{-1}$) were calculated for each stream as described by Meier and Reichert (2005) using average current velocity, channel geometry, channel roughness (Bathurst 1978), slope, and discharge. Differences in A_t and k_{ex} between burn and reference streams were tested using the Mann-Whitney U-test (Zar 1984).

RESULTS

Most habitat variables measured in 1999 were similar between comparably sized streams of burned and unburned catchments (Table 2). For example, cobble-size substrata dominated most streams, although coefficients of variation (CVs) for substrata were higher for some streams of burned catchments than for respective reference streams. Average water depths, substratum embeddedness, and CVs for these variables were comparable between similar-sized streams. Indian Creek was substantially wider (bankfull width) than respective EF L Loon, but this is primarily because of geomorphology and drainage size. Diel temperature recordings indicated little difference between comparably sized burn and reference streams (Fig. 1), although values generally increased with stream size.

Substantial channel scouring was evident for the streams in burned catchments relative to those in unburned catchments in the 20-year study period (Fig. 2). Stream channel change was most evident in burned catchments during the first 10 years following the wildfire, with little additional change obvious during the 2nd decade, suggesting an increase in channel stability. An exception was Little Creek, where additional channel scouring occurred in the latter 10 years. Pungo Creek, the reference for Little Creek, also showed some channel movement during the second 10 years of the study perhaps in response to a wildfire that partially burned its catchment in 1988. Channel profiles for EF Indian and Indian Creeks were essentially unchanged during the 20-year study period. Differences in channel profiles in EF Indian between 1980 and 1988 were likely caused by a change in transect location after that 1st year.

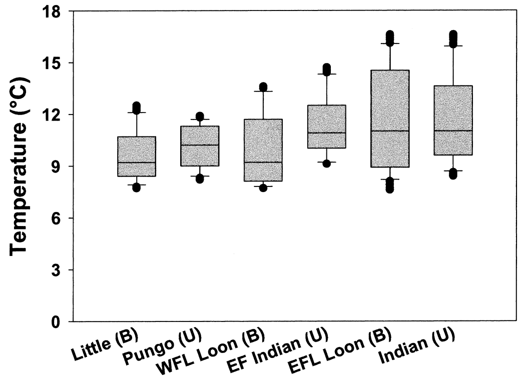

Fig. 1. Box plots of diel water temperatures recorded in midsummer for the study streams: B = burned catchment and U = unburned catchment.

Total volume of large woody debris in streams of burned catchments relative to streams of unburned catchments varied with stream size. Wood volume was essentially the same in burned and reference 2nd-order and 5th-order streams (Fig. 2). However, the volume of large woody debris was ca. 5X greater in the 3rd-order stream in the burned catchment than in the reference stream. In addition, the function of woody debris differed considerably between burn and reference sites with respect to stream size. For example, 80% of the large woody debris was categorized as providing retention in the 2nd-order burn stream, compared to 35% in the reference stream where the majority of woody debris bridged the stream. In contrast, most woody debris was bridging 3rd-order streams (>60%), especially in the burn stream. Last, most large woody debris acted as bridges in 5th-order streams, although the percent bridging was 15% greater in the reference stream.

TABLE 2. Summary statistics for substratum size, water depth, substratum embeddedness, bankfull width, and width:depth ratio for the study streams: B = burned and U = unburned catchment. Sample size was 100 for each, except n = 5 for bankfull width; std = standard deviation, cv = coefficient of variation as %.

	Substratum size (cm)			Depth (cm)			Embeddedness (%)			Bankfull width (m)			Width: Depth ratio
Stream	Mean	std	cv	Mean	std	cv	Mean	std	cv	Mean	std	cv	
Little (B)	10.5	14.9	141	9.0	5.8	65	15.3	26.8	176	2.6	0.6	22	28
Pungo (U)	24.4	20.7	85	14.6	11.2	77	30.8	35.3	115	3.6	0.5	13	24
WF L Loon (B)	18.9	20.0	105	15.9	9.9	62	28.0	27.8	99	5.4	2.3	42	34
EF Indian (U)	18.1	20.0	111	12.1	10.0	83	28.5	30.8	108	3.8	1.4	37	32
EF L Loon (B)	18.2	23.5	129	26.7	13.2	49	31.5	33.3	106	6.5	1.4	21	24
Indian (U)	22.2	21.6	97	31.1	13.8	44	23.8	25.0	105	17.5	1.8	10	56

TABLE 3. Respiration at 20°C and amount of organic matter in bed sediments of study streams. ANOVA table of the comparison between burned and reference sites. Respiration (20°C) O_2 d^{-1} (kg sediment)$^{-1}$. Loosely attached particulate organic matter (LPOM) and organic matter attached to the sediments (AOM) in g AFDM (kg sediment)$^{-1}$.

Parameter	Stream type	Mean	*s*	*F*	*P*-value
Respiration (20°C)	Burn	0.022	0.006	13.41	0.002
	Reference	0.013	0.004		
Total sediment POM	Burn	10.6	3.300	0.15	0.704
	Reference	11.1	1.6		
AOM	Burn	7.0	0.8	25.47	0.0002
	Reference	10.4	1.6		
Total LPOM	Burn	3.95	0.69	11.38	0.004
	Reference	0.78	0.34		
LPOM > 63µm	Burn	2.45	1.60	14.42	0.002
	Reference	0.41	0.21		
LMPM < 63µm	Burn	1.20	1.03	5.77	0.029
	Reference	0.37	0.16		

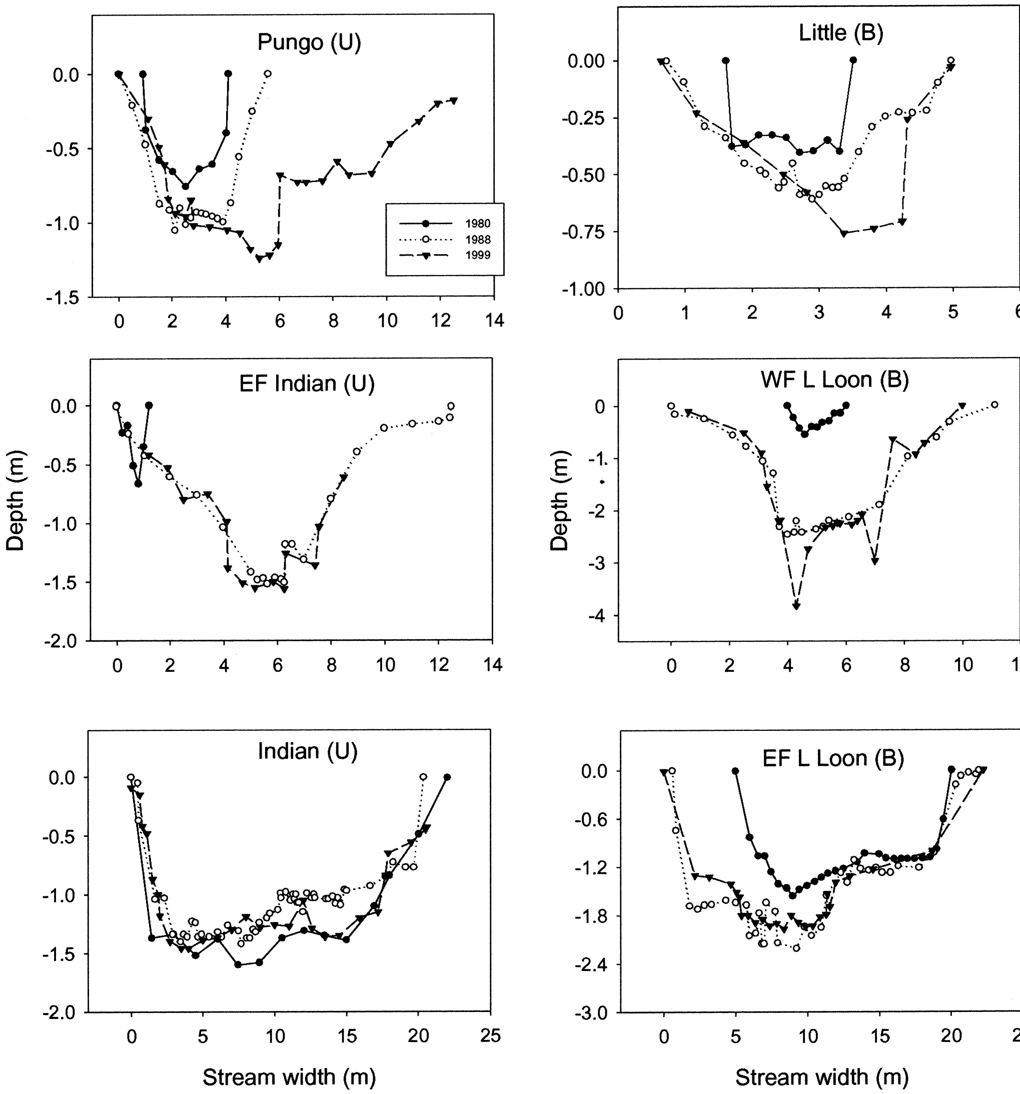

Fig. 2. Cross-sectional profiles for the study streams recorded from a permanent transect installed in 1979. Profiles from 1980, 1988, and 1999 are depicted to represent changes occurring in the first 10 years relative to changes in the second 10 years following the wildfire. Reference streams are indicated by **U** and burned streams by **B**.

Retention of leaves was strongly related to the amount of large woody debris acting as retention devices in each stream. For example, ca. 80% of the released leaves were retained within the first 10 m in Little Creek (Fig. 4), and 80% of the large woody debris recorded in this stream was categorized as having retention capability (Fig. 3). Channel maps indicated that a debris dam was present within this first 10 m that effectively retained the released leaves. In contrast, Pungo Creek retained 80% of released leaves after 50 m, and over 65% of the large woody debris was noted as bridging the stream; no major debris dams were noted in the release reach of Pungo Creek. Woody debris in Pungo Creek likely reflects the impact of miners that lived there around the 1930s or earlier and used the surrounding forest for mining activities. WF L Loon retained <50% of the released leaves in 50 m, and over 80% of its large woody debris was bridging the stream. An increase in retention of leaves in

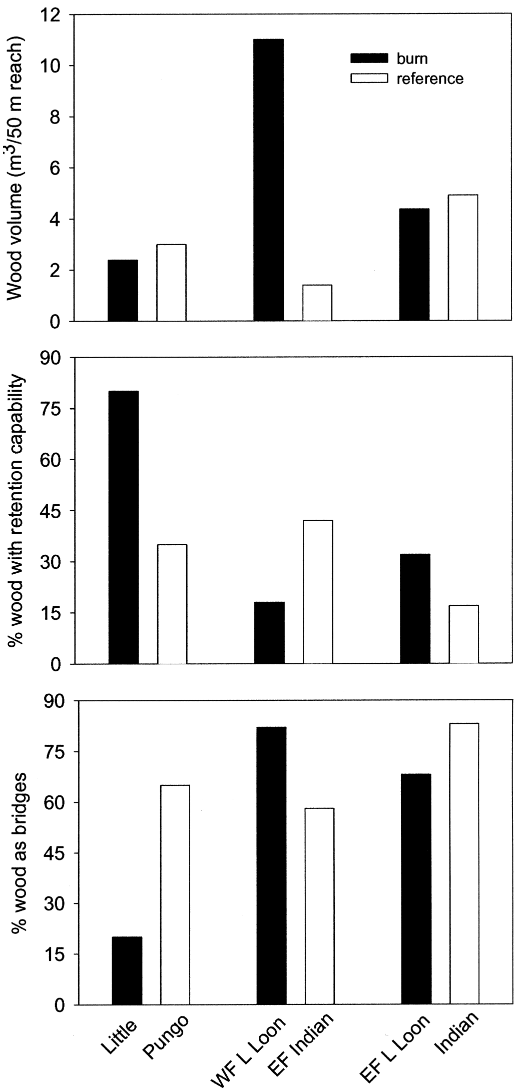

Fig. 3. Bar graphs illustrating total volume of wood within a 50-m reach in the study streams, and percent of this wood categorized as either bridging the stream or contributing to channel stability and retention. Streams are paired by size (stream order).

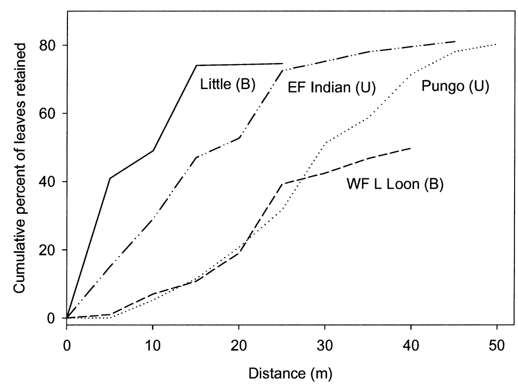

Fig. 4. Cumulative percentage of leaves retained within a 50-m reach in 4 study streams. Logistic constraints prevented this experiment from being conducted in all streams (see Methods).

WF L Loon and EF Indian after about 25 m also was because of a debris dam.

Sediment metabolism, in terms of respiration (mg $O_2 \cdot d^{-1}$), was significantly greater (1.7 X) in streams of burned catchments than in reference streams (Table 3). The total amount of organic matter associated with sediments was similar between burned and unburned streams. However, the amount of organic matter attached to sediments was significantly greater in reference streams than burned streams, whereas the amount of loosely associated organic matter (all measured size fractions) was significantly greater in burned streams (ca. 4–6X as high) than in reference streams (Table 3). Loose organic material is apparently more metabolically active than attached organic matter.

The transient storage zone (A_t) for examined streams ranged between 0.21 and 0.71, averaging 0.43 for burn streams and 0.46 for reference streams. Results of the Mann-Whitney U-test indicated no significant differences between burn and reference streams ($P = 0.83$) for relative sizes of storage zones. However, coefficients of exchange (k_{ex}) were significantly greater in burn streams ($0.0078 \pm 0.0013\ s_{\bar{x}}$) than in reference streams (0.0017 ± 0004; $P < 0.05$).

DISCUSSION

Our results indicate that the functioning of stream ecosystems can be altered over time in response to changes caused by wildfire, a large, infrequent disturbance. Many mid-term changes (1 to >10 years) in stream function are probably a response to the increase in physical disturbance from enhanced peak discharges and sediment input from valley side-slopes the first few years following wildfire (Minshall et al. 1997). Burned streams are expected to become more autotrophic as solar and nutrient inputs are greater and stream temperatures higher than before the fire or later in the recovery sequence (Gresswell 1999, Minshall et al. 2001b), as evidenced by changes in periphyton (Robinson et al. 1994, Minshall et al. 2001b) and macroinvertebrate assemblages (Mihuc and Minshall 1995, Minshall et al. 1997). Spencer and Hauer (1991) documented increased phosphorus and nitrogen loads in streams during wildfire from the smoke and ash from burning vegetation. After >10 years of recovery, burned streams should become increasingly heterotrophic due to decreased solar inputs and increases in allochthonous organic matter as riparian vegetation matures and recovering terrestrial vegetation on valley side-slopes retains surface sediments and water (Minshall and Brock 1991). The increase in side-slope vegetation also should reduce peaks in surface runoff. We found that channels of burned streams, while still structurally simple, became more stable during the second 10 years following fire, and the observed increase in woody debris should enhance structural heterogeneity.

Our results suggest that stream morphology becomes more complex once the large woody debris bridging fire-impacted streams is incorporated into the active stream channel. Wallace et al. (1995) document major channel changes (increases in complexity) in response to adding large woody debris to a stream channel. However, our findings regarding woody debris were strongly related, although nonlinearly, to stream size. There is probably a particular size stream in which the input and utilization of fallen burned timber is maximized; our results suggest that this may occur in mid-order streams as the volume of large woody debris bridging these streams was substantially greater than that observed for the reference stream and other burn streams of different sizes. However, an alternative explanation is the difference in percentage catchment burned among streams of different size. This gradient in percentage catchment burned may influence the degree of woody debris input in later years following wildfire. For instance, Minshall et al. (1997) also found that larger streams had less of their catchment burned than smaller headwater streams. Further, our measures of embeddedness and substratum size were less variable (as CV) in burned streams with lower percentage catchment burned. The exact timing of this enhanced input is likely related to climate; our study was completed in a semiarid environment, suggesting input may be slower than for streams in burned catchments of more temperate climates, e.g., streams in Yellowstone National Park, USA, burned by the 1988 wildfires (see Minshall et al. 1997).

The higher stream complexity from the increase in large woody debris should enhance instream retention as found for forested streams (Bilby and Likens 1980). Our results indicate that retention of leaves is associated strongly with the presence of large woody debris within channels. However, increased channel stability inherent in burned streams during the second 10 years also infers a greater potential for these streams to retain coarse organic matter and thereby enhance their functional efficiency. Indeed, observations of a stream in a similar climate draining a catchment that burned 50 years previously suggests that organic matter retention will become even greater in the next 20–30 years in our study streams (GWM personal observation), especially as riparian vegetation continues to mature and is incorporated into stream channels.

Sediment respiration was significantly higher in streams of burned catchments probably because of the greater amount of loosely attached organic matter in the sediments. Reference and burned streams exhibited similar levels of organic material adhering to sediment surfaces, suggesting that this loosely attached material was of recent origin and provided an important functional component, e.g., a resource for microbes, to these streams. Minshall et al. (1997) showed greater levels of benthic organic matter in streams of burned catchments that were attributed to input from valley side-slopes. This suggests that as stream channels become more stable in burned catchments over time (>10 years), more organic material transferred from terrestrial sources is retained and processed within the system; i.e., the stream becomes more functionally efficient. Minshall et al. (1989) posited that litter inputs will become even greater between 20 and 70 years following wildfire as succession of the terrestrial landscape occurs.

In concordance with sediment respiration results, burn streams had higher coefficients of exchange even though transient storage zones were similar between stream types. The higher k_{ex} likely reflects higher sediment permeability of burn streams, as supported by the greater amount of loosely attached organic matter in the sediment samples of burn streams. This enhanced permeability may have been a result of substantial channel alteration during the first 10 years following the wildfire. In effect, wildfires may indirectly increase hyporheic exchange properties of affected streams by increasing turnover of instream habitats and delivery of smaller substrata by flow disturbances. By maintaining greater porosity of bed sediments, more organic matter can be retained in the system for processing by microbes and other organisms, thus enhancing overall system metabolism.

In summary, wildfire is a major large-scale disturbance in many regions of the world. Because wildfire is an infrequent event, it imposes abiotic and biotic legacies on the landscape. These legacies play important roles in the observed structure and function of stream ecosystems that differ spatially over long periods of time. Our results support previous contentions (e.g., Minshall et al. 1997) that temporal changes in stream structure and function following wildfire are closely associated with successional changes occurring in adjacent terrestrial environments. These temporal changes in the terrestrial environment are transferred to streams via changes in solar radiation and inputs of large woody debris, leaves, and other organic litter that alter channel stability and complexity, organic matter retention and processing, and ultimately ecosystem efficiency.

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LITERATURE CITED

BATHURST, J.C. 1978. Flow resistance of large-scale roughness. American Society of Civil Engineers, Journal of Hydrology Division 104:1587–1603.

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

CATER, F.W., D.M. PINCKNEY, W.B. HAMILTON, R.L. PARKER, R.D. WELDIN, T.J. CLOSE, AND N.T. ZILKA. 1973. Mineral resources of the Idaho Primitive Area and vicinity, Idaho. U.S. Geologic Survey Bulletin 1304.

DAVIS, J.C., G.W. MINSHALL, C.T. ROBINSON, AND P. LANDRES. 2001. Monitoring wilderness stream ecosystems. General Technical Report RMRS-GTR-70, USDA Forest Service, Rocky Mountain Research Station, Ogden, UT. 137 pp.

FOSTER, D.R., D.H. KNIGHT, AND J.F. FRANKLIN. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1:497–510.

GRESSWELL, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the American Fisheries Society 128:193–221.

HARDING, J.S., E.F. BENFIELD, P.V. BOLSTAD, G.S. HELFMAN, AND E.B.D. JONES. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Science 95:14843–14847.

HERSHEY, A.E., G.M. GETTEL, M.E. MCDONALD, M.C. MILLER, H. MOOERS, W.J. O'BRIEN, J. PASTOR, ET AL. 1999. A geomorphic-trophic model for landscape control of arctic lake food webs. BioScience 49: 887–897.

HYNES, H.N.B. 1975. The stream and its valley. Internationale Vereinigung für theoretische und angewandte Limnologie 19:1–15.

JONES, J.B., S.G. FISHER, AND N.B. GRIMM. 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert stream. Ecology 76:942–952.

MEIER, W.K., AND P. REICHERT. 2005. Mountain streams: modelling hydraulics and substance transport. Journal of Environmental Engineering 131.

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

MINSHALL, G.W., D.A. ANDREWS, J.T. BROCK, C.T. ROBINSON, AND D.E. LAWRENCE. 1990. Changes in wild trout habitat following forest fire. Pages 111–119 *in* F. Richardson and R.H. Hamre, editors, Wild Trout IV: proceedings of the symposium. U.S. Government Printing Office 774-173/25037, Washington, DC.

MINSHALL, G.W., AND J.T. BROCK. 1991. Observed and anticipated effects of forest fire on Yellowstone stream ecosystems. Pages 123–135 *in* R.B. Keiter and M.S. Boyce, editors, The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, CT.

MINSHALL, G.W., J.T. BROCK, D.A. ANDREWS, AND C.T. ROBINSON. 2001a. Water quality, substratum, and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek Fire. International Journal of Wildland Fire 10: 185–199.

MINSHALL, G.W., J.T. BROCK, AND J.D. VARLEY. 1989. Wildfire and Yellowstone's stream ecosystems. BioScience 39:707–715.

MINSHALL, G.W., C.T. ROBINSON, AND D.E. LAWRENCE. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, USA. Canadian Journal of Fisheries and Aquatic Sciences 54:2509–2525.

MINSHALL, G.W., C.T. ROBINSON, D.E. LAWRENCE, D.A. ANDREWS, AND J.T. BROCK. 2001b. Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. International Journal of Wildland Fire 10:201–213.

MINSHALL, G.W., T.V. ROYER, AND C.T. ROBINSON. 2004. Stream ecosystem responses following the 1988 Yellowstone wildfires: the first 10 years. Pages 87–97 *in* L. Wallace, editor, After the fires: the ecology of change in Yellowstone National Park. Yale University Press, New Haven, CT.

POFF, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391–409.

ROBINSON, C.T., S.R. RUSHFORTH, AND G.W. MINSHALL. 1994. Diatom assemblages of streams influenced by wildfire. Journal of Phycology 30:209–216.

ROSS, C.P. 1934. Geology and ore deposits of the Casto quadrangle, Idaho. U.S. Geologic Survey Bulletin 854.

SOUTHWOOD, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337–365.

SPENCER, C.N., AND F.R. HAUER. 1991. Phosphorus and nitrogen dynamics in streams during wildfire. Journal of the North American Benthological Society 10:24–30.

SWEENEY, B.W., J.K. JACKSON, J.D. NEWBOLD, AND D.H. FUNK. 1992. Climate change and the life histories and biogeography of aquatic insects in eastern North America. Pages 143–176 *in* P. Firth and S.G. Fisher, editors, Global climate change and freshwater ecosystems. Springer-Verlag, New York.

TONN, W.M. 1990. Climate change and fish communities: a conceptual framework. Transactions of the American Fisheries Society 119:337–352.

TURNER, M.G., W.L. BAKER, C.J. PETERSON, AND R.K. PEET. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

WALLACE, J.B., J.R. WEBSTER, AND J.L. MEYER. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 52:2120–2137.

ZAR, J.H. 1984. Biostatistical analysis. 2nd edition. Prentice-Hall, Inc., Englewood Cliffs, NJ.

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