Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity

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ABSTRACT

Ecohydrological linkages between phosphorus (P) production, stream algae, benthic invertebrate, and fish communities were studied for 4 years after severe wildfire in the Rocky Mountains (Alberta, Canada). Mean concentrations of all forms of P (soluble reactive, total dissolved, particulate, and total) were 2 to 13 times greater in burned and post-fire salvage-logged streams than in unburned streams ($p < 0.001$). Post-disturbance recovery of P was slow with differences in P-discharge relationships still evident 5 years after the fire ($p < 0.001$). Coupled P and sediment interactions were likely responsible for slow recovery of P regimes in fire-disturbed watersheds. P loading was associated with strong ecological responses in stream biota. Annual algal productivity was 5 to 71 times greater in streams within burned watersheds than in reference watersheds and persisted for 5 years after the fire ($p < 0.001$). Elevated algal production was associated with strong differences in benthic invertebrate community structure, including greater invertebrate densities, biomass, species diversity, and shifts in species composition. Monotonic shifts in invertebrate stable carbon and nitrogen isotope ratios indicated increased consumption of autochthonous food sources and effects on energy pathways for invertebrates from fire-affected streams. Wildfire-related changes at lower trophic lead to increases in size (weight and length) and growth rate (weight : age ratios) of cutthroat trout (*Oncorhynchus clarki*). This cascading series of effects of wildfire on stream productivity (primary production, secondary invertebrate consumers, and fish) may be long-lived legacies of wildfire because of the slow recovery of P regimes. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS   forest fire; natural disturbance; hydrologic recovery; stream ecology; phosphorus; sediment; algae; macroinvertebrates

Received 17 October 2013; Revised 11 January 2014; Accepted 21 January 2014

INTRODUCTION

Wildfire is the dominant natural disturbance in many forested landscapes and can produce large and lasting effects on the structure and function of terrestrial and aquatic ecosystems (Weber and Flannigan, 1997; Shakesby and Doerr, 2006; Hauer *et al.*, 2007). Despite considerable research over the past 20 years, far less is known about the magnitude of wildfire-related watershed impacts and factors governing watershed recovery than that of man-made forest disturbances (Ice and Stednick, 2004; Neary *et al.*, 2005). Climate change implicated increases in area burned (Stocks *et al.*, 2002), fire season length, severity, and frequency of wildfires have increased in many regions of the world during recent decades (Flannigan *et al.*, 2005; Westerling *et al.*, 2006), highlighting the need for research on physical, geochemical, and biological effects of wildfires on aquatic ecosystems.

Watershed-scale effects of fire are highly variable and depend on characteristics such as burn severity, intensity, and extent, as well as regional hydro-climatic regimes (Gresswell, 1999). These fire-specific and regional characteristics interact to produce both differential initial responses to wildfire and differing trajectories of recovery (Gresswell, 1999). Effects can include increased magnitude and timing of flow events (Helvey, 1980; Moody and Martin, 2001a, 2001b), elevated concentration or export of

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nutrients (Bladon *et al.*, 2008; Smith *et al.*, 2011), enhanced heavy metal inputs (Kelly *et al.*, 2006), erosion and sedimentation (Kunze and Stednick, 2006; Silins *et al.*, 2009; Moody *et al.*, 2013), and increased light penetration and temperatures in streams (Rhoades *et al.*, 2011; Wagner *et al.*, in press). Changes to physical and geochemical conditions in surface waters can impact in-stream biotic communities through changes in algal productivity (Minshall *et al.*, 2001a), macroinvertebrate abundance and species assemblages (Earl and Blinn, 2003; Minshall, 2003; Spencer *et al.*, 2003), and fish populations (Dunham *et al.*, 2003; Howell, 2006; Kelly *et al.*, 2006). Although wildfires can produce a series of ecohydrologic effects, such as impacts on hydrology, associated changes in geochemical exports, and resultant changes to stream ecology, the vast majority of studies have not collected the data necessary to integrate across several levels of organization to provide a mechanistic understanding of these effects.

One important concern after wildfire is the impact of increased nutrient inputs on water quality. Phosphorus (P) plays an important role regulating primary productivity in lotic ecosystems and to the biogeochemical cycles of other major elements (Mainstone and Parr, 2002; Schindler, 2006). The concentration or production (yield and total export) of various forms of P in aquatic systems increases after wildfire (Prepas *et al.*, 2003; Noske *et al.*, 2010; Smith *et al.*, 2012). Because P often limits the productivity of many aquatic systems (Elwood *et al.*, 1981), post-disturbance P dynamics can form a strong mechanistic link between stream physical/geochemical conditions and their biological communities. The combination of elevated P and greater light availability after loss of shade from the riparian canopy has been associated with increased post-burn algal production (Minshall *et al.*, 2001a). Greater algal production, in turn, is linked to changes in the relative abundance of benthic macroinvertebrates (Earl and Blinn, 2003; Minshall, 2003; Spencer *et al.*, 2003). Thus, hydro-chemical P dynamics can have both direct and indirect effects on primary and secondary producer communities in fire-impacted streams.

Consistent with the conceptual River Continuum Concept (Vannote *et al.*, 1980), both Spencer *et al.* (2003) and Mihuc and Minshall (2005) reported post-disturbance changes to the structure of aquatic food webs. These changes were congruent with shifts in energy pathways by primary consumers, from allochthonous (terrestrial) to autochthonous (in-stream primary production) sources (Spencer *et al.*, 2003; Mihuc and Minshall, 2005). However, the effects of post-fire changes in food sources among disturbance adapted generalist species and trophic specialists (Mihuc and Minshall, 1995) on macroinvertebrate community structure and energy pathways remains unclear. Furthermore, although a growing body of literature describes a range of wildfire effects on individual components of stream hydrologic and ecological responses, cascading ecohydrological responses to wildfire have not been well documented (Spencer *et al.*, 2003). In particular, the incremental effects of post-fire management strategies such as salvage logging remain very poorly described in the literature.

Here we describe an ongoing hydrologic study of the 2003 Lost Creek wildfire that occurred in the Oldman River Basin, a high-water yielding Rocky Mountain headwater system, in southwestern Alberta. The objectives of the present study were as follows: (1) to quantify the initial magnitude of post-fire changes in various forms of P, (2) to document the temporal trend of early P recovery, and (3) to relate these changes to ecological responses by plant and animal communities (algal productivity, benthic macroinvertebrate community structure, and fish growth) in unburned, burned, and post-fire salvage-logged watersheds.

MATERIALS AND METHODS

Study sites

From July to September 2003, the Lost Creek wildfire burned 21 163 ha in both the Castle and Crowsnest River watersheds of the Crowsnest Pass (49°37′ N, 114°40′ W; Figure 1). The wildfire was one of the most severe in southwestern Alberta's Rocky Mountains in many decades. Nearly all forest vegetation and forest floor organic matter in the burned areas were consumed by the fire, with the exception of the Lyons Creek valley where small fire skips left some small, unburned islands of vegetation. The majority of the burned area forms the central headwaters of the Oldman River Basin (the highest water-yielding region of Alberta), which is one of the province's most stressed river systems from a regional water supply and demand perspective (Schindler and Donahue, 2006).

After the wildfire, instrumentation was installed at seven watersheds as part of the Southern Rockies Watershed Project. Three burned watersheds (Lynx Creek, Drum Creek, and South York Creek) and two unburned (reference) watersheds (Star Creek and North York Creek) were instrumented during March–April 2004 (Figure 1). In early 2005, two post-fire salvage-logged watersheds were added to the study (Lyons Creek West and Lyons Creek East). Salvage operations occurred on 261.8 ha in Lyons Creek West (63.4% of the burned area) and 238.2 ha in Lyons Creek East (22.2% of the burned area) between winter 2003/04 and winter 2004/05. All study watersheds have north to northeast aspects with a mean (area-weighted) elevation of 1800 m and a mean area of 823 ha (Table I).
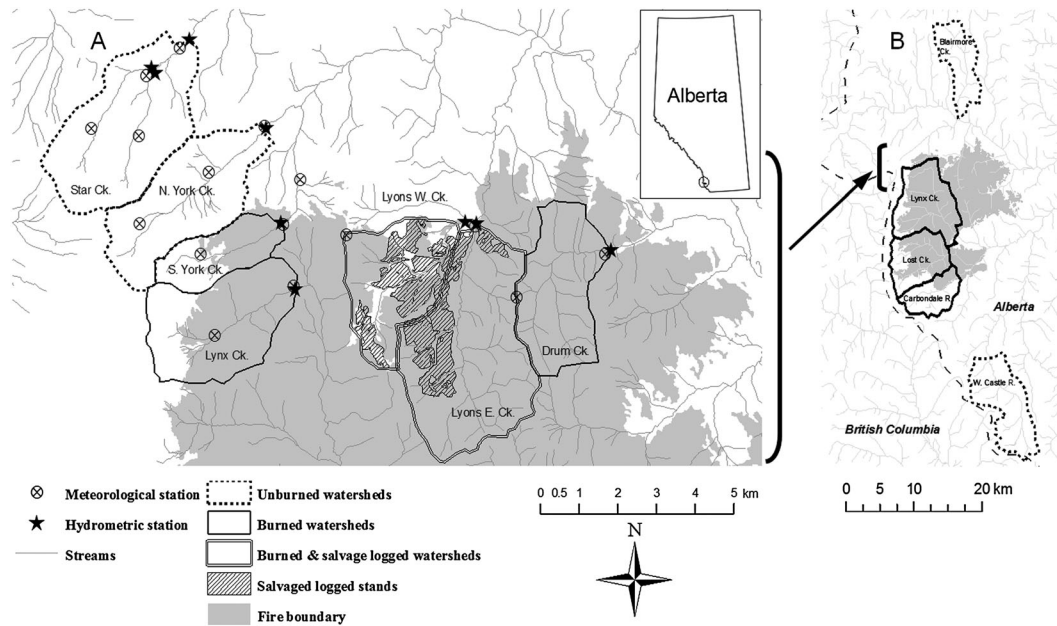
Figure 1. (A) Southern Rockies Watershed Project research watersheds (west to east: Star, North York, South York, Lynx, Lyons West, Lyons East, and Drum), including boundary of the 2003 Lost Creek wildfire (grey), and (B) regional watersheds (burned and reference) used for fish sampling in September 2005. Arrow indicates region in map A corresponding to the larger regional watersheds in map B.

Table I. Characteristics of Southern Rockies Watershed Project study watersheds.

Watershed	Total Area (ha)	Area burned (ha/% burned)	Elevation (m; mean/range)	Watershed slope (%)	Channel slope (%)
Unburned (reference)					
Star	1035	0 (0.0)	1851 (1479–2627)	45.0	10.5
North York	865	2 (0.2)	1931 (1562–2633)	48.8	14.8
Burned					
South York	365	191 (52.3)	1971 (1691–2635)	42.1	8.3
Lynx	781	553 (70.8)	1906 (1632–2629)	43.3	5.9
Drum	718	712 (99.2)	1731 (1432–2156)	47.5	9.3
Burned and salvage logged					
Lyons (east)	1309	1072 (81.9)	1685 (1441–2027)	31.8	5.0
Lyons (west)	684	413 (60.4)	1666 (1449–2059)	24.8	7.2

Montane, subalpine, and alpine ecozones are represented within all watersheds. Prior to the fire, the forests were dominated by Lodgepole pine (*Pinus contorta* var. *latifolia*) at lower elevations (upper montane), Engelmann spruce (*Picea engelmanii*) and Subalpine fir (*Abies lasiocarpa*) at mid-elevations (subalpine), and alpine meadow vegetation and bare rock at higher elevations (alpine). Because of the absence of tree cover (fuel loading), alpine areas were generally not burned in the fire. Thus, although the proportion of total watershed area burned varies from 53 to 100%, forest cover and riparian vegetation in the watersheds were almost completely consumed by the fire. Surficial geology of the watersheds is dominated by Cretaceous shales and sandstones overlain by well to imperfectly drained soils (Brunisols) with weak horizon development characteristic of higher elevation northern environments. All study watersheds were similar in slope, aspect, elevation range, soils, geology, and forest cover before the wildfire.

Water quality sampling

Water sampling was conducted year-round beginning in April 2004. Manual, depth-integrated water samples were collected during snowmelt freshet (approximately every 10 days), post-freshet summer through fall (every 14 days), and throughout winter (every 1 to 1.5 months), with additional sampling during periodic stormflow events (ice-free seasons). This resulted in approximately 18 to

25 water samples per watershed each year. Stream water samples were collected approximately 10 m upstream of hydrometric gauging stations (Figure 1). Depth-integrated samples were collected in acid-washed (10% HCl) triple-rinsed high-density polyethylene bottles that were refrigerated at 4 °C and transported to the laboratory for analyses within 4 days after collection.

Stream discharge was measured concurrently with the water quality samples using a Swoffer (Model 2100) velocity meter and standard area–velocity current metering techniques. Stage–discharge relationships were developed from stage measured with staff gauges at each site. Continuous stream discharge was determined using stage–discharge relationships at each gauging station applied to continuous records of stage measured using gas bubblers (Waterlog model H-350) or pressure transducers (Onset model U-20).

Total P (TP; unfiltered), total dissolved P (TDP; 0.45 μm filter), and soluble reactive P (SRP) concentrations were determined by automated ascorbic acid reduction (Method $4500 - P : F$) using a Lachat QuikChem 8500 multi-channel flow injection analyzer (Greenberg *et al.*, 1999). TP and TDP samples were digested by persulfate oxidation with potassium persulfate ($K_2S_2O_8$). Particulate P (PP) was calculated as the difference between TP and TDP.

Algae sampling

Beginning in April 2005, periphyton samples were collected immediately upstream of the gauging stations in each of the seven streams by deploying three replicate unglazed porcelain tiles ($155 \, cm^2$ surface area) in mid-stream riffles. Fixed-area samples were collected by scraping and rinsing tiles into plastic scintillation vials once each month (May to October). Periphyton was frozen until fluorometric analysis of chlorophyll *a* (Chl*a*) (Sartory and Grobbelar, 1984) and determination of ash-free dry mass (AFDM) (Aloi, 1990).

Benthic macroinvertebrate sampling and stable isotope analysis

Benthic macroinvertebrates were sampled in early October 2007. Benthos sampling (Surber sampler; $0.09 \, m^2$) occurred upstream of hydrometric gauging sites from undisturbed riffle reaches in each of the seven streams. Site selection was based on uniformity of streambed gradient, bed material (cobble size: 5 to 15-cm diameter), water depth (5-cm to 10-cm depth), and velocity. Samples were collected from the entire width of the streambed. For each replicate (4–6 per stream), individual stones were rubbed clean and removed from the sample area. The bed material was then vigorously disturbed for 2 min, after which the contents of the Surber sampler were washed through a 500-micron sieve and rinsed. Macroinvertebrate samples were immediately preserved in 95% ethanol in polyethylene Nalgene bottles (125 ml).

In the laboratory, a dissecting scope was used to identify specimens to the lowest possible taxonomic group (usually Genus), which were then assigned to morphospecies (Clifford, 1991). The functional feeding group (filterer, shredder, scraper, or predator) of each specimen was determined on the basis of ecological information from various sources (Wiggins and Mackay, 1978; Dieterich and Anderson, 1995; Voshell and Wright, 2002). Taxa for stable isotopes analysis (SIA) were chosen if sufficient homogeneous material among taxa was present to provide the modest replication for each functional group in reference, burned, and salvage-logged streams. When necessary, individual specimens (1–10 individuals) of the same taxa and replicate samples were pooled to obtain sufficient biomass for SIA. Prior to SIA, all samples were treated with 1 N HCl using the drop-by-drop method to remove any potential carbonates (Jacob *et al.*, 2005), oven-dried in aluminum boats at 60 °C for 24 h, and ground with a 250-ml glass mortar and pestle. Ground samples were stored in plastic centrifuge tubes at room temperature prior to SIA.

Stable isotopes analysis involves determination of ratios of naturally occurring heavy and light stable isotopes for various elements, and comparison to the ratios of a primary standard for the same element. The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic composition of macroinvertebrates was determined by flash combustion using a Costech ECS 4010 Elemental Combustion System (Costech Analytical Technologies Inc., Valencia, CA) coupled to a continuous flow Isotope Ratio Mass Spectrometer (Finnigan Delta Plus Advantage, ThermoFinnigan, Bremen Germany). The isotopic composition of the samples was calculated from

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000\%o \quad (1)$$

where $\delta^{13}C$ or $\delta^{15}N$ are expressed in permil (‰) units. R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample, and R_{standard} is the ratio in the standard. For carbon, the working standards were BMO, CS, NBS 1575 N, and Red Clover, with a carbon isotope composition of −23.91, −12.5, −26.3, and −27.42‰ relative to the Pee Dee Belemnite carbonate standard, respectively. For nitrogen, the working standards were also BMO, CS, NBS 1575, and Red Clover, with a nitrogen isotope composition of 8.2, 9.1, 0.907, and −0.56‰ relative to air, respectively.

Fixation of freshwater invertebrate samples with ethanol results in small increases in both $\delta^{13}C$ (mean ± SD: 1.18 ± 0.94) and $\delta^{15}N$ (0.39 ± 0.68) (Ventura and Jeppesen, 2009). Because all samples collected for this study were preserved with ethanol, within-study comparisons are valid. Similar fixation methods were used prior to SIA in Spencer *et al.* (2003).

To compare the trophic position of invertebrate consumers among streams, variability in baseline $\delta^{15}N$ must be removed by baseline adjustment. This is particularly important in aquatic systems affected by forest fire, which can cause baseline $\delta^{15}N$ variability (e.g. Kelly *et al.*, 2006). The use of scrapers as baseline organisms has been suggested for rivers (Anderson and Cabana, 2007). We subtracted the $\delta^{15}N$ of scrapers from the $\delta^{15}N$ of other functional feeding groups within each replicate invertebrate sample. To assess baseline $\delta^{15}N$ differences between treatments, we calculated baseline $\delta^{15}N$ as the unadjusted $\delta^{15}N$ of an organism minus the adjusted $\delta^{15}N$ of an organism. For watersheds affected by forest fire and salvage logging, we also subtracted the mean $\delta^{15}N$ of scrapers from reference streams (0.02‰). Pre-fire baseline values were not available for streams affected by forest fire and salvage logging, so the mean $\delta^{15}N$ of scrapers from reference streams was the best available indicator of baseline conditions; stream characteristics that may have influenced baseline $\delta^{15}N$ before fire and salvage logging were similar.

Fish sampling

Fish were collected by electrofishing streams within burned, post-fire salvage-logged, and reference watersheds at the end of September 2005. Because of limited road access, different streams than were sampled for water quality, algae, and invertebrates that reflected reference and disturbed conditions were sampled (Figure 1). A total of 104 individuals of cutthroat (*Oncorhynchus clarki*) and rainbow trout (*Oncorhynchus mykiss*) were sampled; however, cutthroat trout were present in the reference streams (Blairmore Creek, West Castle River) and burned streams (Lost Creek, Lynx Creek, and Carbondale River), but not in the post-fire salvage-logged stream sampled (Lyons Creek). In contrast, rainbow trout were present only in one reference stream (Blairmore Creek) and one salvage-logged stream (Lyons Creek), but were not present in any of the three burned creeks sampled. Because occurrence of the two fish species were confounded across the three disturbance categories, we present data only for cutthroat trout from two reference streams and three burned streams. For each stream, a 200-m to 300-m stream reach was sampled by electrofishing. Weight and fork length of all individuals were recorded before killing and freezing fish for subsequent removal of otoliths in the laboratory to determine age. Otoliths were soaked in 99% ETOH and 50% glyceryn for 2–3 weeks to aid in visual determination of fish age. Two measures of cumulative growth rate were calculated: (1) the ratio of fish weight : age and (2) fork length : age.

Statistical analyses

Statistical analyses were performed using the SAS statistical package (Version 9.1, SAS Institute Inc., Carey, NC), except for invertebrate community analyses, which were performed using R (Version 2.4.1, The R Foundation for Statistical Computing). Non-parametric techniques (Helsel and Hirsch, 2002) were used to evaluate 'treatment' effects because the distributions of water quality variables (various P forms) and measures of algal productivity (AFDM and Chl*a*) were not normal despite attempts at data transformation (log, log($x + 1$)), or arcsine (square root(x)). A series of single factor Kruskal–Wallis tests and Dunn's mean comparison tests were used to analyse the effects of the 'treatments' (reference, burned, and post-fire salvage-logged) and time (years elapsed since the fire) on the concentration of the various forms of P (SRP, TDP, PP, and TP) and periphyton production (AFDM and Chl*a*).

Total P–stream discharge relationships were compared among 'treatment' groups using tests for coincidental regression for each year from 2004 to 2007 (e.g. overall test for slopes and intercepts) after Zar (1999).

Individual-based rarefactions were used to compare estimates of species richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT) between reference, burned, and post-fire salvage-logged watersheds (Hurlbert, 1971). The EPT assemblages were further described using an agglomerative hierarchical clusters technique that used Euclidean distances and Ward's Method on log($x + 1$)-transformed data to construct a dendrogram of community similarity in the different streams (McCune and Grace, 2002). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes were compared between functional feeding groups (scrapers: Heptageniidae and *Ameletus*; shredders: *Yoraperla*; filterers: Hydropsychidae; predators: Perlidae, Perlodidae, Rhyacophilidae) and between the reference, burned, and post-fire salvage-logged watersheds using analysis of variance (ANOVA) followed by a Tukey's post hoc test (Zar, 1999).

Differences in fish size and growth rates between reference and burned streams were compared by ANOVA. Streams nested within 'treatment' were used as the error variance for testing the effects of fire disturbance. Although the age class distribution of fish differed among streams, 2-year-old and 3-year-old fish were common to all streams; thus, these age classes were used in the ANOVAs for fish size and growth rate.

RESULTS

Precipitation and discharge

Mean annual precipitation across the seven watersheds was 1059 mm (2004–2007) (Table II), with the greatest annual precipitation generally occurring in the higher elevation Flathead Range watersheds (Star, North York, South York, and Lynx Creeks). Approximately 50 to 70% of the total annual precipitation fell as snow from October to April. There was considerable variation in the meteorological

Table II. Annual precipitation (mm year^{-1}) and streamflow (mm year^{-1}) in the study watersheds during 2004–2007.

		Year				
	Watershed	2004	2005	2006	2007	Mean
Precipitation	Unburned (reference)	1264	1321	872	877	1084
	Burned	1106	1455	1003	965	1132
	Burned and salvage-logged	–	1097	1017	661	925
Streamflow	Unburned (reference)	663	1001	598	571	708
	Burned	871	1003	761	760	849
	Burned and salvage-logged	–	720	535	584	613

conditions over the first four post-fire growing seasons. The first post-burn growing season (2004) was cool and moist with 0.1–5 mm precipitation day^{-1} for 55% of days – but generally without any notably large summer precipitation events. In contrast, there were several extremely large rainfall events in June 2005 (~150–175 mm of rain over 8 days). These events saturated soils and produced significant streamflow responses to smaller subsequent precipitation events. The third (2006) and fourth (2007) post-fire years were increasingly hot and dry with no measurable precipitation observed from early June until late September.

Discharges were generally characteristic of high water yielding Rocky Mountain streams. Mean annual streamflow across the seven watersheds averaged 741 mm during the four study years (Table II). Mean annual runoff ratios during the four years of study were 74% (range: 43 – 97%), with greater ratios (> ~80%) generally observed in the steeper, higher elevation watersheds along the Flathead Range (Star, North York, South York, and Lynx Creeks). Hydrologic regimes in all of the watersheds were dominated by the spring snowmelt freshet, with the highest streamflows generally occurring during the snowmelt freshet (mean daily discharges of ~7–10 mm day^{-1}), which extended from about mid-March until mid-June. Most rainstorm hydrographs were characterized by rapid time to rise and steep post-peak recession limbs. Strong stream groundwater inputs produced steady fall and overwinter baseflows of approximately 0.5–2.0 mm day^{-1} in all streams. Some of the more extreme flow events were produced by periodic rain-on-snow or mid-winter melt events, which resulted in mean daily discharges up to 28 mm day^{-1}.

Stream water chemistry

Concentrations of all forms of P (SRP, TDP, PP, and TP) differed strongly among reference, burned, and post-fire salvage-logged streams ($p < 0.001$) for the 4 years of study. The concentrations of all forms of P were consistently greater in the burned streams compared with the reference streams in all 4 years (Figure 2), whereas streams in salvage-logged watersheds consistently produced the greatest concentrations of all forms of P. The largest

differences in P concentrations between disturbed (burned and post-burned salvage-logged) and reference watersheds (2004–2007) were observed for PP and TP. Mean concentrations in burned streams were 7.4 and 5.8 times greater than in unburned streams for PP and TP, respectively (Table III). Concentrations of PP and TP in streams exposed to salvage logging were 8.3 and 7.4 times greater than streams in reference watersheds, respectively (Table III). Although disturbance effects on soluble forms of P were not as strong as those evident with particulate forms, the effect of wildfire and post-fire salvage logging was still substantial with 3.7-fold (SRP) and 3.4-fold (TDP) mean differences evident between burned and reference watersheds, whereas 6.7-fold (SRP) and 6.1-fold (TDP) mean differences were observed between salvage-logged and reference watersheds for the four study years (Table III). Virtually all of the greatest P concentrations observed in this study (upper tenth percentile) occurred in disturbed watersheds (burned and post-burn salvage-logged), including 96% of the highest PP and TP concentrations and 100% of the highest SRP and TDP concentrations.

Elevated P concentrations were observed during the two wetter years immediately after the fire (2004 and 2005) and during higher runoff periods within each year (snowmelt freshet and storms). Strong variation in concentrations of SRP, PP, and TP was observed among study years ($p < 0.01$); however, multiple comparisons tests indicated that this was primarily driven by greater concentrations during 2005 (wettest year) compared with the two increasingly dry years of 2006 and 2007 ($p < 0.01$). Similarly, variation in concentration of SRP, TDP, PP, and TP within seasons was driven by strongly elevated P production during snowmelt and stormflow events compared with baseflow conditions ($p < 0.001$). Concentrations of TP during higher flow events (snowmelt and stormflow) were 2.5 times (unburned: 8.5 µg l^{-1}), 8.5 times (burned: 82.7 µg l^{-1}), and 4.9 times (salvage-logged: 74.5 µg l^{-1}) greater than during baseflow periods.

These patterns parallel variation in TP production observed across the dominant hydrologic seasons for this region. TP was greater in both burned and post-fire salvage-logged watersheds across a range of stream discharges
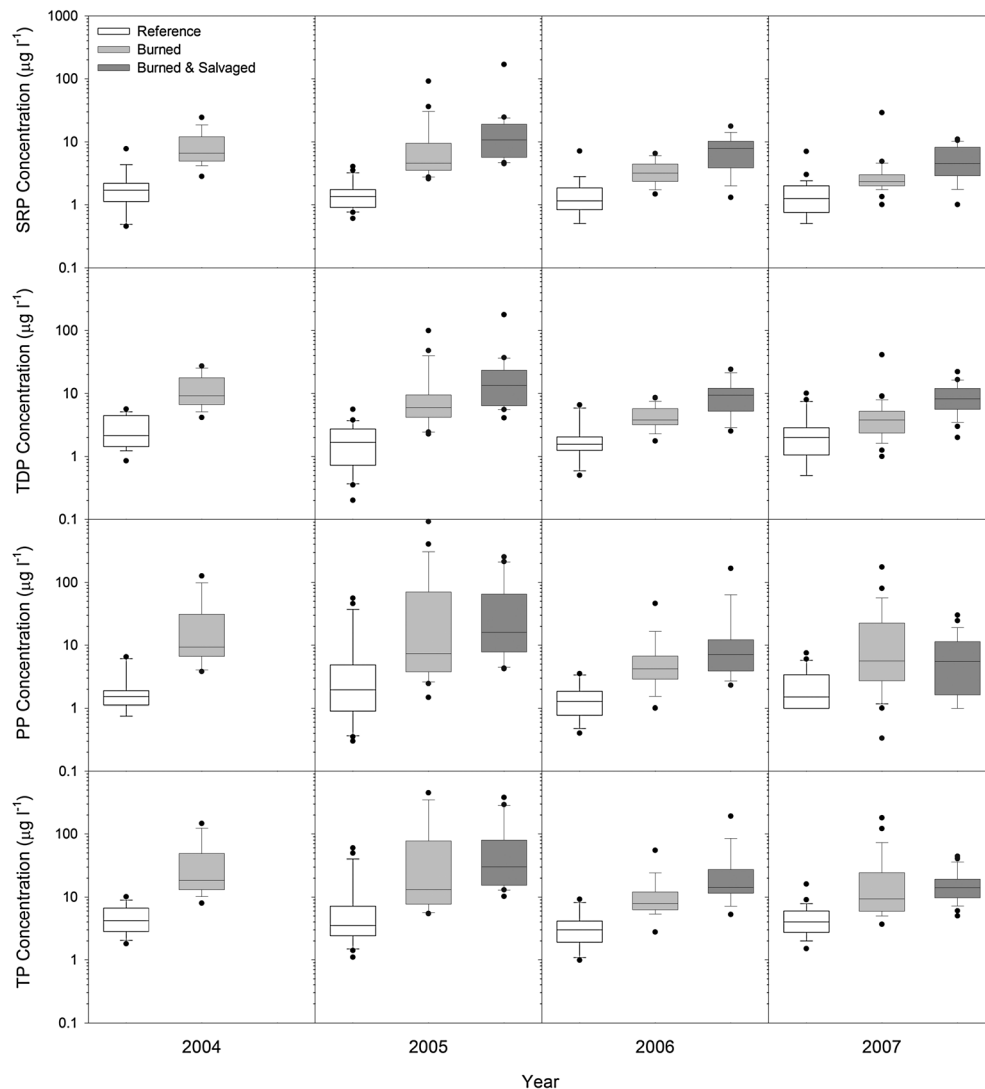
Figure 2. Box and whisker plots of soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), particulate phosphorus (PP), and total phosphorus (TP) concentrations ($\mu g\,l^{-1}$) from the unburned (reference), burned, and post-fire salvage-logged watersheds from 2004 to 2007.

(TP–Q relationships; Figure 3) for all 4 years after the fire ($p < 0.001$) although the upward shift in TP–Q relationships was stronger in post-fire salvage-logged watersheds than in burned watersheds during each year of study (Figure 3). Whereas the dissolved P fraction (TDP and SRP) was elevated during high-flow events, the majority of increases in the TP concentrations at higher discharges were driven by strongly elevated PP during snowmelt and/or stormflow events. Mean PP concentrations during stormflow events were 7 times (unburned: $9.8\,\mu g\,l^{-1}$), 25 times (burned: $131.8\,\mu g\,l^{-1}$), and 11 times (salvage-logged: $71.4\,\mu g\,l^{-1}$) greater than during baseflows (non-event periods). Particulate P accounted for 55% (unburned), 71% (burned), and 65% (salvage-logged) of TP production during snowmelt and stormflow events, compared with 43% (unburned), 48% (burned), and 39% (salvage-logged) of TP production during baseflow periods.

Differences between concentrations of all forms of P in streams from disturbed and unburned watersheds decreased since the time of disturbance, yet recovery was slow (Table III). For example, in 2005, the TP concentration was 6.9 times (burned) and 9.0 times (burned and salvage-logged) greater in disturbed watersheds. By 2007, these differences had diminished but were still 3.6 times (burned) and 3.8 times (salvage-logged) greater in disturbed than unburned watersheds. A similarly weaker temporal pattern of post-disturbance recovery in the disturbed watersheds was evident for TDP, SRP, and PP (Table III). However, because of the decline in precipitation over the four study years (Table II), decline in mean slope in the TP–Q relationships from 2004 to 2007 (Figure 3) was more strongly associated with variation in seasonal precipitation rather than indicating a clear trend of post-disturbance P recovery.

Table III. Mean nutrient concentrations ($\mu g\,l^{-1}$) and standard error (in brackets) for soluble reactive phosphorus (SRP), dissolved organic phosphorus (DOP), total dissolved phosphorus (TDP), particulate phosphorus (PP), and total phosphorus (TP) in the reference, burned, and post-fire salvage-logged streams from 2004 to 2007.

Nutrient	Year	Reference	Burned	Salvage-logged
SRP	2004	2.0 (0.3)	9.0 (1.4)	
	2005	1.5 (0.1)	8.3 (2.0)	19.2 (5.3)
	2006	1.6 (0.3)	3.5 (0.3)	7.6 (0.8)
	2007	1.3 (0.2)	3.0 (0.5)	5.6 (0.5)
DOP	2004	1.2 (0.3)	2.8 (0.5)	
	2005	0.7 (0.2)	1.8 (0.4)	3.5 (0.6)
	2006	0.7 (0.3)	1.0 (0.2)	2.4 (0.5)
	2007	1.2 (0.3)	1.6 (0.3)	3.7 (0.4)
TDP	2004	2.8 (0.3)	11.8 (1.6)	
	2005	1.8 (0.2)	9.7 (2.3)	22.2 (5.7)
	2006	2.0 (0.4)	4.4 (0.4)	9.9 (1.1)
	2007	2.5 (0.4)	4.6 (0.7)	9.2 (0.8)
PP	2004	2.0 (0.4)	24.9 (8.3)	
	2005	7.2 (2.4)	52.0 (21.8)	58.5 (13.9)
	2006	1.5 (0.2)	7.3 (1.5)	19.0 (6.5)
	2007	2.2 (0.4)	12.0 (3.6)	7.8 (1.1)
TP	2004	4.8 (0.5)	36.7 (9.6)	
	2005	9.0 (2.5)	61.7 (24.1)	80.7 (17.6)
	2006	3.5 (0.5)	11.7 (1.8)	28.8 (7.3)
	2007	4.5 (0.5)	16.2 (3.7)	16.9 (1.5)

Algal production

Algal production, as reflected by AFDM, was strongly elevated in burned and post-fire salvage-logged watersheds compared with reference watersheds from 2005 to 2007 ($p < 0.001$) and was similar when burned and post-fire salvage-logged watersheds were compared ($p = 0.15$) (Figure 4). The mean annual AFDM in burned watersheds was 14.3 times greater in 2005 ($0.24\,\mathrm{mg\,cm^{-2}}$), 8.5 times greater in 2006 ($0.22\,\mathrm{mg\,cm^{-2}}$), and 9.8 times greater in 2007 ($0.16\,\mathrm{mg\,cm^{-2}}$), than reference watersheds. The mean annual AFDM in salvage-logged watersheds was 5.4 times higher in 2005 ($0.09\,\mathrm{mg\,cm^{-2}}$), 7.2 times higher in 2006 ($0.19\,\mathrm{mg\,cm^{-2}}$), and 11.1 times higher in 2007 ($0.19\,\mathrm{mg\,cm^{-2}}$), compared with reference streams.

Similarly, chlorophyll a (Chl$a$) concentrations in burned and post-fire salvage-logged watersheds were greater than those in reference watersheds from 2005 to 2007 ($p < 0.001$), but similar Chl$a$ were seen within the burned and salvage-logged watersheds ($p = 0.48$) (Figure 4). The mean annual Chl$a$ concentrations in burned watersheds were 71 times greater in 2005 ($0.16\,\mu\mathrm{g\,cm^{-2}}$), 25 times greater in 2006 ($0.0048\,\mu\mathrm{g\,cm^{-2}}$), and 18 times greater in 2007 ($0.68\,\mu\mathrm{g\,cm^{-2}}$), than in reference watersheds. The mean annual concentration of Chl$a$ in salvaged-logged streams was 33 times higher in 2005 ($0.07\,\mu\mathrm{g\,cm^{-2}}$), 23 times higher in 2006 ($0.0045\,\mu\mathrm{g\,cm^{-2}}$), and 17 times higher in 2007 ($0.64\,\mu\mathrm{g\,cm^{-2}}$) compared with the reference streams.
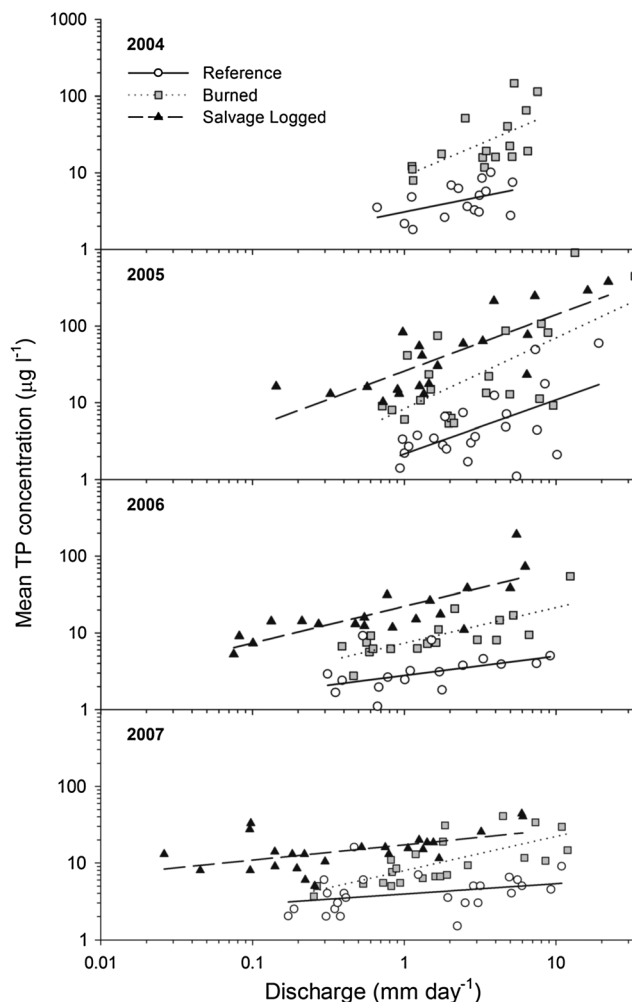

Figure 3. Regression relationships between mean total phosphorus (TP) concentration ($\mu g\,l^{-1}$) and discharge ($\mathrm{mm\,day^{-1}}$) from the unburned (reference), burned, and post-fire salvage-logged watersheds from 2004 to 2007.

Benthic macroinvertebrate communities

A total of 2527 macroinvertebrates, representing 20 Families and 33 Genera, were collected and identified from the study streams in 2007. The patterns of abundance, richness, and community structure showed clear differences between streams in burned and post fire salvage-logged watersheds, compared with reference streams. The abundance of benthic macroinvertebrates (per unit area) was highest in post fire salvage-logged streams (125.0 ± 19.6), followed by burned streams (63.4 ± 6.8), and lowest in the unburned streams (43.2 ± 6.7) (Figure 5). Mean biomass of individuals was also greater in fire-affected streams: burned ($90.4\,\mathrm{mg}$) > salvage-logged ($57.0\,\mathrm{mg}$) > reference ($46.1\,\mathrm{mg}$). The ratio of macroinvertebrates sensitive to disturbance-related changes in water quality conditions (EPT) to less sensitive macroinvertebrates (Diptera [D]) differed strongly among stream disturbance categories. The ratio of EPT:D per Surber sample was 268.9 ± 67.4 in
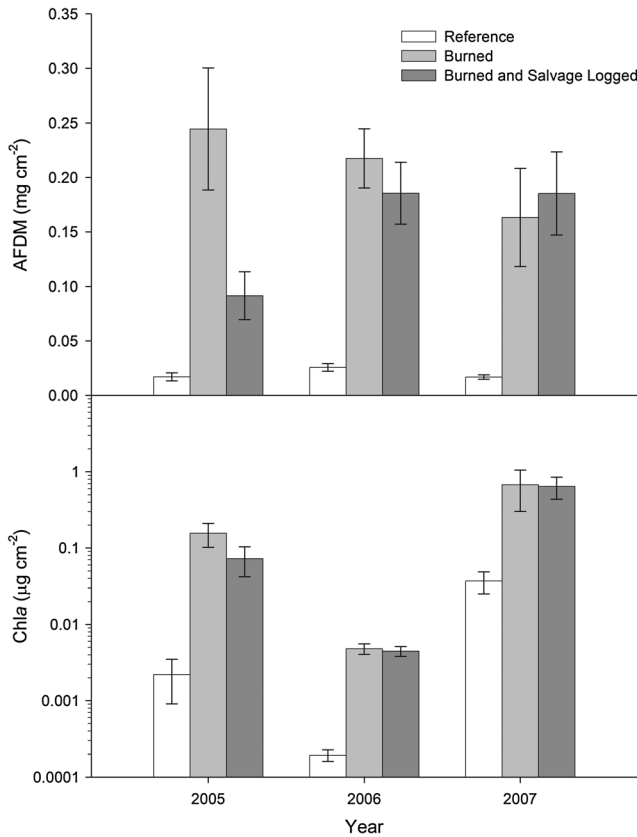
Figure 4. Periphyton biomass as mean annual ash free dry mass (AFDM; mg cm^{-2}) and chlorophyll a (Chl$a$; μg cm^{-2}) concentrations from the unburned (reference), burned, and post-fire salvage-logged watersheds from 2005 to 2007. Errors bars indicate one standard error of the mean.

reference streams, compared with 14.6 ± 3.6 and 5.4 ± 1.1 in burned and post-fire salvage-logged streams, respectively (Figure 5). Benthic macroinvertebrate species richness was also greatest in the salvage-logged watersheds and least in unburned watersheds. Estimates of richness were 23.2 ± 1.3 for post-fire salvage-logged streams, 22.1 ± 1.0 for burned streams, and 16.9 ± 0.3 for unburned streams. Cluster analysis also indicated a difference in community composition for streams within salvage-logged, burned, and reference watersheds (Figure 6).

Differences in the proportional representation of each functional feeding group among unburned, burned, and post-fire salvaged-logged streams were also evident. The proportion of shredders in burned streams (24%) was approximately 3 times higher than in unburned streams (8%). Conversely, the proportion of scrapers was lower in burned (13%) and post-fire salvage-logged streams (15%) compared with unburned streams (44%). Predators accounted for the highest proportion of individuals in most streams with 55% in post-fire salvage-logged, 41% in burned, and 39% in unburned streams. The proportion of gatherer/collectors in post-fire salvage-logged streams (21%) was much higher than observed in burned (4%) or unburned streams (4%).
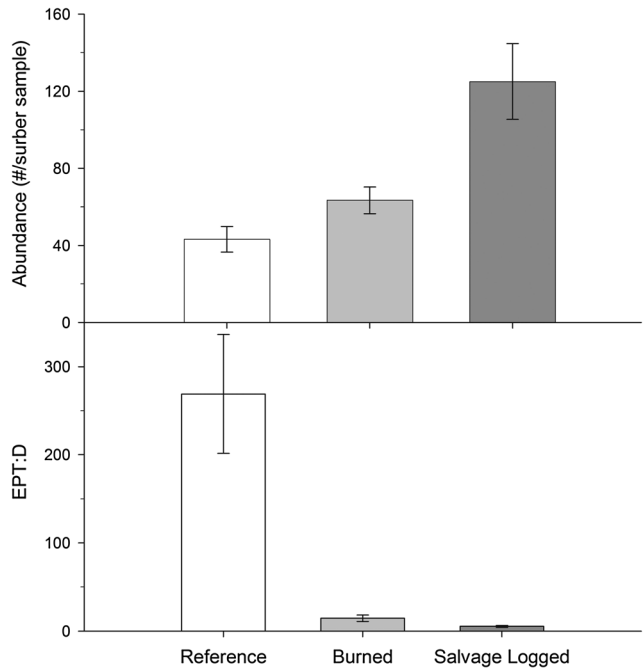

Figure 5. Macroinvertebrate abundance (number of individuals per Surber sample [0.09 m^2]) and the ratio of macroinvertebrates sensitive to disturbance-related changes in water quality conditions (Ephemeroptera, Plecoptera, Trichoptera [EPT]) to less sensitive macroinvertebrates (Diptera [D]).
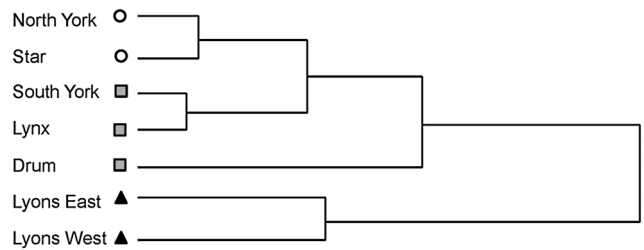

Figure 6. Cluster analysis dendrogram for Euclidean distances between Ephemeroptera, Plecoptera, and Trichoptera benthic macroinvertebrate communities in unburned (circles), burned (squares), and postfire salvage-logged (triangles) watersheds in 2007.

Benthic macroinvertebrate stable isotope analyses

We observed a strong influence of wildfire and post-fire salvage logging on $\delta^{15}N$ and $\delta^{13}C$ of benthic macroinvertebrates ($p < 0.001$, Figure 7). The mean $\delta^{15}N$ of macroinvertebrates was greatest in streams within watersheds affected by salvage logging ($5.62‰ \pm 0.17$) followed by streams in burned watersheds ($3.99‰ \pm 0.17$) and was lowest ($1.17‰ \pm 0.21$) in reference streams ($p < 0.001$, Figure 7). Enrichment of $\delta^{13}C$ occurred ($p < 0.001$) in both the burned ($-30.16‰ \pm 0.23$) and post-fire salvage-logged watersheds ($-30.02‰ \pm 0.30$), when compared with reference watersheds ($-33.16‰ \pm 0.23$) (Figure 7). No significant difference in $\delta^{13}C$ of macroinvertebrates was identified between streams within burned and salvage-logged watersheds
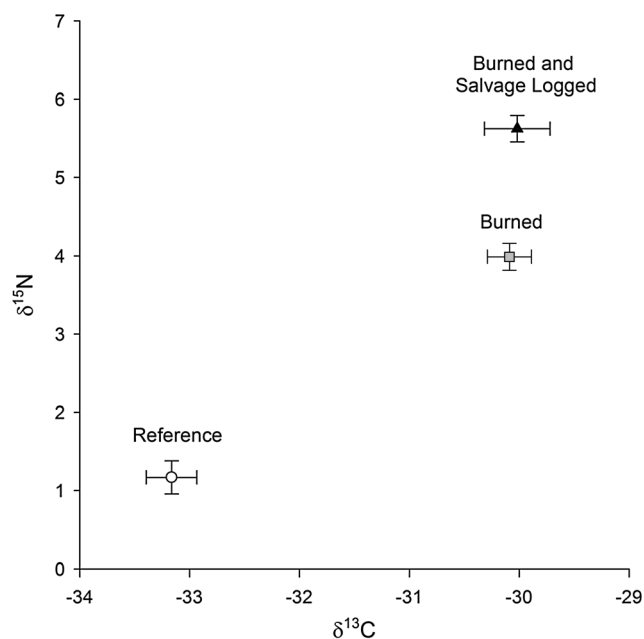
Figure 7. Bi-plot of stable isotope compositions (δ^{13}C and δ^{15}N; ‰) of benthic macroinvertebrates from unburned (reference), burned, and post-fire salvage-logged watersheds in 2007.

Figure 8. Stable isotope compositions (δ^{13}C and δ^{15}N; ‰) of benthic macroinvertebrates by functional feeding group (shredders, scrapers, filterers, and predators) from unburned (reference), burned, and postfire salvage-logged watersheds in 2007.

($p = 0.73$). The average enrichment of δ^{15}N was 2.8‰ in the burned and 4.5‰ in the post-fire salvage-logged watersheds, whereas the average increase in δ^{13}C was 3.1‰ in both the burned and salvage-logged watersheds compared with the reference watersheds.

Within functional feeding groups, both δ^{15}N and δ^{13}C were greater in streams within burned and post-fire salvage-logged watersheds, than streams in reference watersheds ($p < 0.001$, Figure 8). The general pattern of δ^{15}N and δ^{13}C within macroinvertebrate functional feeding groups was reference < burned < post-fire salvage-logged. Among functional feeding groups, neither the δ^{15}N of scrapers and shredders ($p = 0.76$) nor the δ^{15}N of filterers and predators ($p = 0.33$) was significantly different. However, the δ^{15}N of scrapers and shredders was significantly lower than that of filterers and predators ($p < 0.001$). No significant differences in δ^{13}C were found between shredders and predators ($p = 0.87$), shredders and filterers ($p = 0.56$), and filterers and predators ($p = 0.14$), yet the δ^{13}C of scrapers was significantly greater than filterers ($p < 0.001$), shredders ($p = 0.03$), and predators ($p = 0.05$).

Small differences among treatments in the baseline-adjusted δ^{15}N of macroinvertebrates (an indicator of food web effects) were also evident. Within treatments, the pattern of baseline-adjusted δ^{15}N was shredders predators < filterers for both the reference and burned streams. In salvage-logged watersheds, the pattern differed (shredders < filterers < predators). However, the only significant difference was a decrease in the baseline-adjusted δ^{15}N of invertebrates in salvage-logged streams when
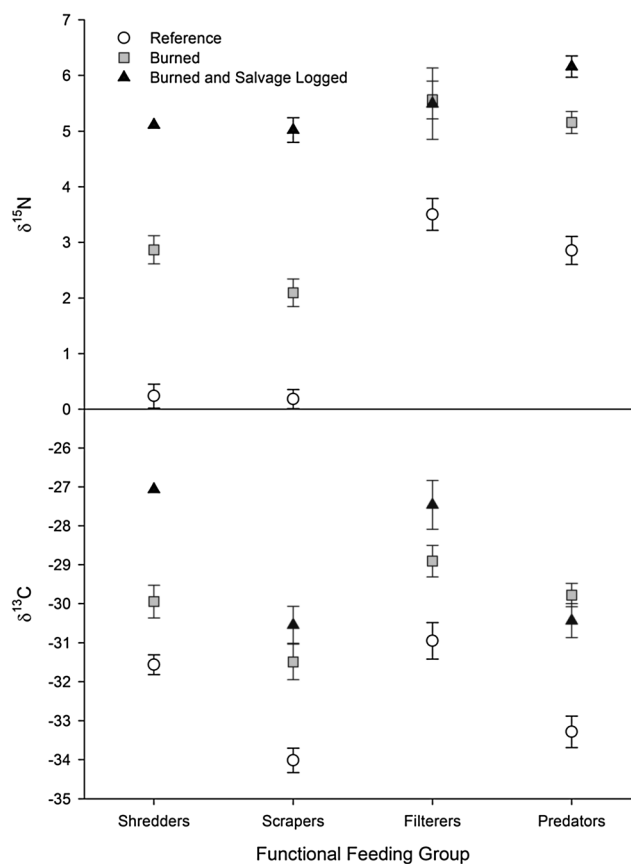
compared with burned or reference streams ($p < 0.001$). The mean baseline δ^{15}N of invertebrates in burned streams (2.3‰) was significantly lower than that of salvage-logged watersheds (4.6‰, $p < 0.001$).

Fish growth

Although fish age class was strongly associated with differences in size and cumulative growth rates of cutthroat trout (Figure 9), no interactions between age class and disturbance category were evident for size (mass and length) or cumulative fish growth rate variables ($p = 0.42$–0.52); thus, age classes were pooled to determine the disturbance effects on fish size and growth rate.

Cutthroat trout (2-year and 3-year age classes) from burned streams were larger and grew more rapidly than fish from reference streams although the effect of the wildfire on fish weight was notably stronger than effects on fish length (Figure 9). Fish from burned streams weighed more ($p = 0.014$) and had greater cumulative weight : age growth ratios ($p = 0.009$) than fish from nearby reference streams. In contrast, the effect of the wildfire on total fish length was slightly weaker ($p = 0.026$), and no effect on cumulative length : age ratio was evident ($p = 0.10$).
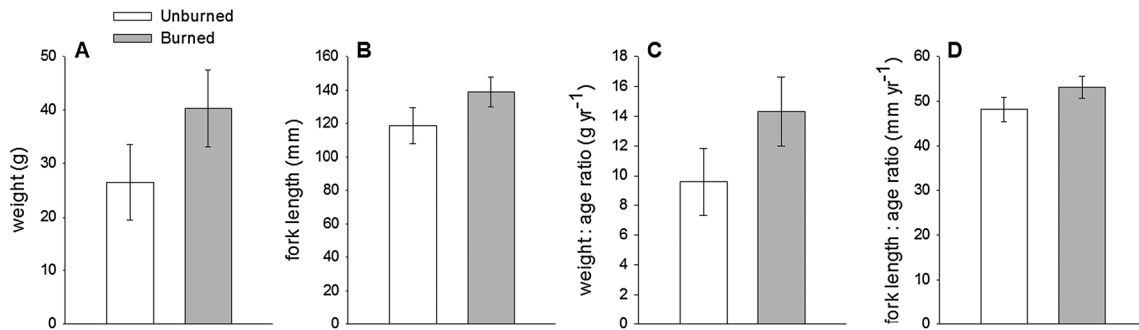
Figure 9. (A) Fresh weight, (B) fork length, (C) cumulative weight : age growth rate, and (D) cumulative length : age growth rate of 2-year-old to 3-year-old cutthroat trout (*Oncorhynchus clarki*) from burned and reference streams ~2.5 years after the wildfire.

DISCUSSION

This work demonstrates that landscape disturbance from wildfire and post-fire management interventions such as salvage logging can produce cascading chemical, physical, and biological responses that extend from lower trophic levels (primary producers) through secondary consumer communities.

Stream water chemistry

Wildfire and salvage logging resulted in greater (2 to 13 times) mean annual concentrations of all forms of P (SRP, TDP, PP, and TP) in the disturbed watersheds compared with the unburned watersheds in each of the four years after the fire (2004 to 2007) (Table III; Figure 2). Elevated P concentrations for several years after wildfire are consistent with other studies of different environments and forest types; however, the magnitude of the differences we observed between disturbed and reference watersheds were in the upper range of post-wildfire effects. For example, mean annual TP concentrations observed in this study were 3 to 8 times greater in burned and 4 to 9 times greater in salvage-logged compared with unburned watersheds. In contrast, Tiedemann *et al.* (1978) reported 2 to 3 times greater mean TP concentrations in streams after wildfire in northcentral Washington, and Schindler *et al.* (1980) observed 1.4 to 3.2 times greater mean TP concentrations after wildfire in boreal shield watersheds of northwestern Ontario, whereas Lane *et al.* (2008) observed up to fivefold to sixfold differences in TP concentrations between burned and reference eucalypt forest watersheds in southeastern Australia.

Similarly, the median and maximum P concentrations also constitute some of the highest post-wildfire P concentrations reported in the literature (<60–206 $\mu g\,l^{-1}$; Gluns and Toews, 1989; Bayley *et al.*, 1992; Hauer and Spencer, 1998). In contrast, maximum TP concentrations were 1122 $\mu g\,l^{-1}$ in the burned watersheds and 401 $\mu g\,l^{-1}$ in the salvage-logged watersheds. The greatest TP concentrations occurred during the highest discharge events in all watersheds; however, we

also observed a clear upward shift in the TP-discharge regime across the full range of streamflow in both burned and post-fire salvage-logged watersheds (Figure 3). The severity of the fire and high proportion of watershed area burned in the 2003 Lost Creek wildfire was likely a strong contributor to the elevated P production we observed in comparison to previous studies. Higher regional precipitation and steep topographic relief (e.g. both longitudinal and side valley relief) of headwater watersheds promote strong hydrologic gradients that drive both surface and subsurface flow paths (Harman *et al.*, 2009) producing potentially stronger coupling between the burned landscape and stream-water quality. Moreover, surficial geology of the region dominated by glacial deposition of sedimentary fine-grained till blankets and veneers is likely an important factor in stronger sediment-P transport and channel storage interactions compared with regions with more coarse grained surficial geology.

Phosphorus is widely known to have strong storage and exchange interactions with sediment and particulate matter (Froelich, 1988), consistent with our observations that a large proportion of TP production was in particulate (PP) form in all watersheds. Whereas the TP concentration was elevated during higher discharge events (Figure 3), higher PP concentration and decreased TDP : PP ratios during high streamflows (e.g. snowmelt freshet and stormflow events) coincided with periods of peak sediment production (Silins *et al.*, 2009). In the present study, maximum PP concentrations (unburned: 61 $\mu g\,l^{-1}$; burned: 1015 $\mu g\,l^{-1}$; salvage-logged: 364 $\mu g\,l^{-1}$) were strongly associated with maximum sediment concentrations (unburned: 78 $mg\,l^{-1}$; burned: 1429 $mg\,l^{-1}$; salvage-logged: 378 $mg\,l^{-1}$), which were observed during several large rainfall events in June 2005 (~150–175 mm of rain over 8 days). Wildfires can lower erosion thresholds (Benavides-Solorio and MacDonald, 2001), resulting in substantially increased sediment production in burned watersheds (Ewing, 1996; Kunze and Stednick, 2006). Increased PP production during snowmelt and stormflow events was most evident in salvage-logged (26% increase over baseflow) and burned watersheds (23%), compared with unburned watersheds (12%). Thus,

the large changes in sediment regime and increased sediment production in burned and post-wildfire salvage-logged watersheds (Silins *et al.*, 2009) were strongly associated with greater seasonal variation in P production in burned and post-fire salvage-logged watersheds. The observation of greater P production in salvage-logged watersheds is not surprising given that salvage logging (including linear disturbances associated with logging roads) represents an incremental landscape disturbance over that of wildfire alone (Silins *et al.*, 2009).

The temporal pattern of P recovery after disturbance by wildfire and salvage logging is also likely to be governed by the strong coupling of sediment-P storage and transport dynamics. The concentrations of all forms of P in disturbed watersheds appeared to decline very slowly towards values similar to reference watersheds (Figure 2 and 3). However, this apparent recovery may be confounded by precipitation and runoff generation in the two most recent years of the study (2006 and 2007), which were comparatively dry (below average). It is likely that sediment-P linkages may extend the duration of impacts from disturbances, such as wildfire, which increase the potential for erosion and sedimentation. Although PP is not immediately bioavailable, the legacy of the adsorbed fraction of P can become an important long-term source for aquatic ecosystems, after release from particle surfaces into the water column (Froelich, 1988; Ellison and Brett, 2006). Moreover, in the present study region, downstream transport of sediment from the burn were associated with ~70% greater bioavailable forms of P (non-apatite inorganic P) compared with unburned stream reaches (Allin *et al.*, 2012). Thus, exchange processes between sediment associated and aqueous P are important factors in overall nutrient and contaminant transport and storage and their linkage to biogeochemical recovery after disturbances such as wildfire (Stone *et al.*, 2014).

We found that SRP, one of the most readily usable forms of P by primary producers (Hatch *et al.*, 1999), was also strongly elevated in disturbed watersheds. SRP concentrations were greater than $3 \mu g \, l^{-1}$ for 68% of all observations in burned watersheds and 80% of all observations in salvage-logged watersheds, whereas SRP concentration was consistently below $3 \mu g \, l^{-1}$ (94% of observations) in the unburned watersheds for 4 years after the fire. SRP concentrations in reference watersheds were similar to those reported for oligotrophic streams in the Rocky Mountains of Montana (Spencer and Hauer, 1991). Similar to our study, mean annual SRP ranged from 2 to 6 times greater in burned streams than control streams up to 5 years after wildfire in the Rocky Mountains of Glacier National Park in Montana (similar climate, elevation, relief, soils, and vegetation composition as our study) (Hauer and Spencer, 1998).

Phosphorus and its interaction with other major elements frequently limit primary productivity in freshwater environments (Elwood *et al.*, 1981; Hart and Robinson, 1990). The nitrogen to P ratios (mean N : P ratios from 2004 to 2007: unburned 75:1, burned 60:1, salvaged 21:1 [N from the present study site, Bladon *et al.*, 2008]) indicated that P was likely the most limiting nutrient for the headwater streams in the present study. In a similar hydro-climatic setting, Chessman *et al.* (1992) found that P was the limiting factor for aquatic production in forested sub-alpine environments when the N : P ratio was greater than 17:1. Thus, as many stream water quality parameters were elevated following the Lost Creek wildfire (Bladon *et al.*, 2008; Silins *et al.*, 2009; Emelko *et al.*, 2011), increased P production was the most likely factor responsible for clear differences in primary and secondary production we observed between reference and fire-disturbed streams (burned and post-fire salvage-logged). These impacts to headwater streams would also be expected to have impacts on downstream riverine environments (Stone *et al.*, 2011).

Biotic response

Primary producers responded dramatically to P enrichment in the post-fire and post-salvage-logged watersheds. During the spring immediately after the wildfire (2004), thick mats of algae appeared on streambeds in the disturbed watersheds, whereas little, if any, algal growth was evident in unburned watersheds. Our results clearly indicated elevated algal productivity (AFDM and Chl*a*) in the disturbed watersheds from 2005 to 2007 (Figure 4). We anticipate that primary productivity will remain elevated for several more years because of the elevated TP–discharge regime (Figure 3). Moreover, increased light exposure due to loss of riparian vegetation in fire-disturbed streams will likely continue to stimulate growth of autotrophic stream production (Mihuc and Minshall, 2005) until light penetration to stream surfaces is limited because of riparian vegetation re-growth. As our results are generally consistent with observations of post-fire increases in algal production elsewhere, the longevity of these effects appear quite variable in the literature. Algal productivity approximately tripled in all burned streams 2 years after wildfire in a high-elevation mixed-conifer forest in central Idaho but returned to reference levels 5 years post-fire (Minshall *et al.*, 2001a). In contrast, Mihuc and Minshall (2005) reported 10 years of elevated post-fire algal productivity after a severe wildfire in Yellowstone National Park. Post-fire algal production was depressed in a number of streams because of the steep relief and high streamflows that resulted in physical disturbance of the stream channel after the 1988 fire season in Yellowstone (Minshall *et al.*, 1997). Despite these varied observations, the increase in primary production after major disturbances, such as wildfire or forest harvesting, is

generally consistent with increased nutrient loading (Hauer *et al.*, 2007).

Increased autochthonous food sources (in-stream algae) in the present study likely contributed to elevated benthic macroinvertebrate abundance after the Lost Creek fire. Invertebrate abundance was approximately 1.5 times greater in the burned streams and 2.9 times greater in the salvage-logged streams compared with the reference streams 4 years after the wildfire (Figure 5). We also observed greater invertebrate biomass, species richness, and a lower EPT/D ratio in fire-disturbed streams compared with reference streams, which generally reflected greater numbers of disturbance-adapted strategists or trophic generalists (e.g. D; Figure 6). This is consistent with reports of greater abundance, richness, and diversity in wildfire-affected streams 45 years after a wildfire in Yellowstone National Park (Albin, 1979) and with observed shifts in benthic fauna community structure favouring disturbance adapted taxa (Minshall *et al.*, 1997; Minshall *et al.*, 2001b). However, observations have been highly variable with several studies reporting decreased macroinvertebrate abundance and richness after fire as a result of direct (mortality) and indirect effects (e.g. high flow events, sedimentation) (Minshall *et al.*, 2001b; Minshall, 2003). After wildfires in central Idaho, New Mexico, and Arizona, taxa richness and/or total abundance were also lower in burned compared with reference streams; this was largely attributed to the physical changes of the stream (e.g. major channel cutting, sediment scouring, ash input) (Rinne, 1996; Minshall *et al.*, 2001a; Earl and Blinn, 2003). Roby and Azuma (1995) found greater macroinvertebrate abundance, but they also observed lower taxon richness in burned streams compared with reference streams in all 11 years after a wildfire in northern California.

The δ^{15}N and δ^{13}C signatures of macroinvertebrates from burned and post-fire salvage-logged watersheds were clearly elevated compared with reference watersheds (Figure 7). This provides strong evidence that wildfire and post-fire salvage logging can significantly influence the energy pathways of aquatic food webs (Rounick *et al.*, 1982; Hamilton *et al.*, 2004). The average baseline-adjusted enrichment of δ^{15}N for invertebrates from burned watersheds was 2.3‰ (unadjusted = 2.8‰) and from the post-fire salvage-logged watersheds was 4.6‰ (unadjusted = 4.5‰) compared with reference watersheds. Our results are consistent with other studies analysing stable nitrogen isotopes from macroinvertebrates after wildfire in forested headwater streams. The δ^{15}N of macroinvertebrates was 2.8‰ greater in burned streams compared with reference streams from Yellowstone National Park (Mihuc and Minshall, 2005) and was 0.5‰ greater in burned streams from Glacier National Park, Montana (Spencer *et al.*, 2003). Post-fire enrichment in δ^{15}N of the aquatic invertebrates is believed to be due to a shift from allochthonous to autochthonous energy sources (internally derived periphyton), which were in greater abundance in fire-impacted streams. Although δ^{15}N in autochthonous resources was not quantified in this study, reviews of other stable isotope studies have reported clear, monotonic enrichment in ^{15}N in autochthonous food sources compared with detrital (i.e. allochthonous) food sources (France, 1995b; Peipoch *et al.*, 2012). Another alternative mechanism that could explain the increase in δ^{15}N in invertebrates from fire impacted streams is increased assimilation of fine particulate organic matter or partially burned allochthonous plant material with elevated δ^{15}N signatures. Although less plausible, this alternative explanation requires additional research to elucidate the effects of wildfire on shifts in aquatic food webs and on isotopic ratios of allochthonous and autochthonous resources in lotic systems.

The δ^{13}C of macroinvertebrates was also enriched in burned watersheds (3.0‰) and post-fire salvage-logged watersheds (3.1‰) compared with reference watersheds (Figure 7). We speculate that this likely indicates consumption of more autochthonous food sources. However, δ^{13}C is less reliable than δ^{15}N as an indicator of dietary shifts in consumer organisms because it is often highly variable with overlapping δ^{13}C signatures among allochthonous and autochthonous food sources (Rounick *et al.*, 1982; France, 1995a; Spencer *et al.*, 2003). Not surprisingly, previous studies on the effects of wildfire on δ^{13}C in stream macroinvertebrates have reported widely variable results. Both increased δ^{13}C (this study; Mihuc, 2004; Mihuc and Minshall, 2005) and decreased δ^{13}C (Spencer *et al.*, 2003; Kelly *et al.*, 2006) of invertebrates have been reported following fire, but all were attributed to increased use of autochthonous energy sources. However, in this study, terrestrial organic matter inputs after the wildfire resulted in 31 times greater particulate organic C in bed sediments of burned creeks (burned: 1.57%/g bed material; unburned: 0.05%/g bed material) (Stone *et al.*, 2011); thus, invertebrates in fire-disturbed streams could have increased their use of partially burned allochthonous food sources. Indeed, a great deal of burned and partially burned organic material intrusion was observed in the interstitial voids of fire-disturbed streambeds. Future research should quantify the δ^{13}C of these potential food sources to clarify the impacts of fire on energy pathways for primary consumers.

Lastly, the increases in algal and macroinvertabrate productivity after wildfire were associated with increases in size and growth rate of cutthroat trout living in these streams. The Lost Creek wildfire reached its full extent in July–August 2003; thus, the 2-year to 3-year age classes of cutthroat trout (spring spawners) we sampled in the fall of 2005 essentially grew entirely in a wildfire-affected environment. Effects of the wildfire on P production, algal productivity, and subsequent increases in abundance of benthic macroinvertebrates food sources for fish would be expected to take some time to produce measurable changes

in fish growth; thus, the greater size and growth of fish from burned streams were surprising. Whereas a large number of researchers have studied the initial impacts of wildfire or fire suppression on fish populations in western North America (Gresswell, 1999) or explored impacts on fish population dynamics (Dunham *et al.*, 2003; Rieman *et al.*, 2003; Howell, 2006), reports of direct effects of fire on fish growth are limited. The increases in fish size and growth 3 years after the fire that we identified are consistent with Koetsier *et al.* (2007) who observed larger (weight and length) rainbow trout in burned streams compared with reference streams 12–14 years after wildfire in Idaho (USA). Although some report rapid recovery of fish populations (Rieman and Clayton, 1997) after fire, longer term P-sediment storage dynamics, as well as their association with greater primary and secondary productivity in burned streams, will likely lead to long-term elevated fish growth in our study streams.

CONCLUSION

Results from this study clearly show a cascading series of ecohydrological effects of wildfire that link this severe disturbance to (1) increased geochemical production of P in previously oligotrophic streams, (2) clear subsequent increases in primary productivity of algal communities, in turn leading to (3) subsequent increases in benthic macroinvertebrate abundance and species diversity at several trophic levels (herbivore, detritivore, predator), and lastly, leading to (4) increased size and growth rate of one of the key aquatic predators (cutthroat trout) in these streams. We also observed incremental effects of salvage logging, over and above that of wildfire, at each step in this series of ecohydrologic effects. Furthermore, our results indicate that aquatic ecological effects of wildfire may be long lived because P-sediment interaction will likely mediate P storage dynamics for a long time. Large and severe wildfires in western North America, from California northward into western Canada, have occurred during the last decade. These wildfires have been responsible for a range of impacts on hydrology and water quality, including impacts on human water uses. The occurrence of large and severe wildfires and the length of fire season are expected to increase with climate change. This highlights the need for research on the effects of these large landscape-scale disturbances on water, ecosystem responses, and impacts on a range of human water needs.

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