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Fire and Aquatic Ecosystems in Forested Biomes of North America

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Abstract.—Synthesis of the literature suggests that physical, chemical, and biological elements of a watershed interact with long-term climate to influence fire regime, and that these factors, in concordance with the postfire vegetation mosaic, combine with local-scale weather to govern the trajectory and magnitude of change following a fire event. Perturbation associated with hydrological processes is probably the primary factor influencing postfire persistence of fishes, benthic macroinvertebrates, and diatoms in fluvial systems. It is apparent that salmonids have evolved strategies to survive perturbations occurring at the frequency of wildland fires (10^0–10^2 years), but local populations of a species may be more ephemeral. Habitat alteration probably has the greatest impact on individual organisms and local populations that are the least mobile, and reinvasion will be most rapid by aquatic organisms with high mobility. It is becoming increasingly apparent that during the past century fire suppression has altered fire regimes in some vegetation types, and consequently, the probability of large stand-replacing fires has increased in those areas. Current evidence suggests, however, that even in the case of extensive high-severity fires, local extirpation of fishes is patchy, and recolonization is rapid. Lasting detrimental effects on fish populations have been limited to areas where native populations have declined and become increasingly isolated because of anthropogenic activities. A strategy of protecting robust aquatic communities and restoring aquatic habitat structure and life history complexity in degraded areas may be the most effective means for insuring the persistence of native biota where the probability of large-scale fires has increased.

Fire is widely recognized as an agent of disturbance and ecological change (Wright 1974; Pickett and White 1985; Knight 1987), and numerous studies have described the effects of fire on vegetation, soils, nutrients, water yield, and erosion (e.g., Fredriksen 1971; Beschta et al. 1987; Troendle and Bevenger 1996). The results of investi-

gations before the mid-1980s have been the subject of several review papers (e.g., Ahlgren and Ahlgren 1960; Kozlowski and Ahlgren 1974; Mooney et al. 1981). Fire research during this period often examined the effects of prescribed fires (including slash burns following clear-cut logging) on site productivity, vegetation regeneration, and succession (e.g., Tiedemann et al. 1979; Wright and Bailey 1982). In general, early studies were site specific, and little attention was given to the effects of fire at landscape or regional scales or the role

of fire in ecosystem function. Studies that addressed effects of fire on aquatic ecosystems focused on the loss of soil through erosion and changes in water yield and quality (Anderson 1976; DeBano et al. 1977; Tiedemann et al. 1979). Before the late 1980s, only a few studies had considered the effects of fire on the biotic communities of aquatic systems (Heinselman 1973; Wright and Heinselman 1973; Wright 1976).

The size and severity (severity is related heat transferred to soils and the general effect on biological systems; Brown 1990) of fires in the Greater Yellowstone Ecosystem in 1988 (Christensen et al. 1989) and in central Idaho in 1992 and 1994 (Rieman et al. 1997a) and growing concern about the health and management of low-elevation conifer forests of the western United States, where fires have been suppressed (Covington et al. 1994; Quigley et al. 1996), have stimulated renewed interest in the effects of fire (e.g., Young 1994; Rinne 1996; Minshall et al. 1997). Natural variability of disturbance (Reice et al. 1990; Swanson et al. 1994), changes in land use and fire suppression associated with Euro-American settlement (Gruell 1985), impacts of global warming on fire frequency (Balling et al. 1992; Price and Rind 1994), and the influence of ecosystem management on fire regimes and forest health (Quigley et al. 1996; Rieman and Clayton 1997) are important current issues for resource managers. The role of fire in aquatic ecosystems is directly related to many of these concerns, and there has been a substantial increase in research evaluating the biological consequences of fire in streams during the past decade.

The purpose of this paper is to review the recent literature regarding the effects of fire on aquatic ecosystems. In the first section, the specific effects (i.e., physical, chemical, and biological) of fire on aquatic systems are reviewed with emphasis on research occurring since the mid-1980s. The second section attempts to synthesize the results of specific studies and discuss the role of fire in aquatic ecosystems in general.

Effects of Fire on Aquatic Ecosystems

Effects of fire on aquatic systems may be direct and immediate (i.e., pulsed disturbance; Yount and Niemi 1990) or indirect and sustained over an extended period (i.e., press disturbance; Yount and Niemi 1990). Beyond the actual fire event, Minshall et al. (1990) suggested that effects of fire can be separated into midterm and long-term consequences. Midterm effects peak within the first decade following the fire when changes are most dra-

matic, but long-term effects coincide with the revegetation of burned areas. Ultimately, however, the effects are constrained by fire size and intensity (intensity refers to upward heat transfer and mortality of aboveground vegetation; Brown 1990), postfire weather (primarily precipitation and wind), and physical, chemical, and biological characteristics of individual sites (Figure 1).

Direct Effects

One direct effect of fire is biomass reduction. The area affected by fire is related to fire size and intensity, and physical and climatic variables that influence the spread and intensity of fire. Following the 1988 fires in the Greater Yellowstone Ecosystem, Turner et al. (1994) found that the proportion of the total area in different burn severity classes varied with daily fire size. The pattern was least predictable and most heterogeneous when fires were small, and at this scale, the controlling variables included fuel moisture, fuel type, atmospheric humidity, wind, temperature, and topography. On days when more than 1,250 ha burned, heterogeneity was lower because the main controlling variables were wind velocity and direction, and during those periods, the pattern of burn severity was highly predictable (Turner et al. 1994).

Although the size of individual fires varies among forested regions of North America, the area burned is often relatively small (Hunter 1993; Brown et al. 1994). Most forest fires burn less than 1 ha (Pyne 1984), and 1% of the total number of fires accounts for 80–96% of the total area burned (Strauss et al. 1989). During a 17-year period (1971–1987) under a management policy that allowed lightning-ignited fires to burn in Yellowstone National Park (Sellers and Despain 1976), 503 fire starts burned a total area of 14,566 ha; the annual area burned exceeded 2 ha/fire start only four times during that period (Turner and Romme 1994). In contrast, Turner and Romme (1994) reported that 24 natural ignitions burned 292,000 ha in the region during the extreme fire conditions of 1988 (Schullery 1989).

Mortality of fish and aquatic invertebrates is another direct effect of fire that has been reported (Table 1). Minshall and Brock (1991) reported dead salmonids in three small streams in Yellowstone National Park following the fires of 1988. The simultaneous occurrence of live fish in these streams (G. W. Minshall, Idaho State University, personal communication) suggests that mortality was not uniform or that surviving individuals mi-
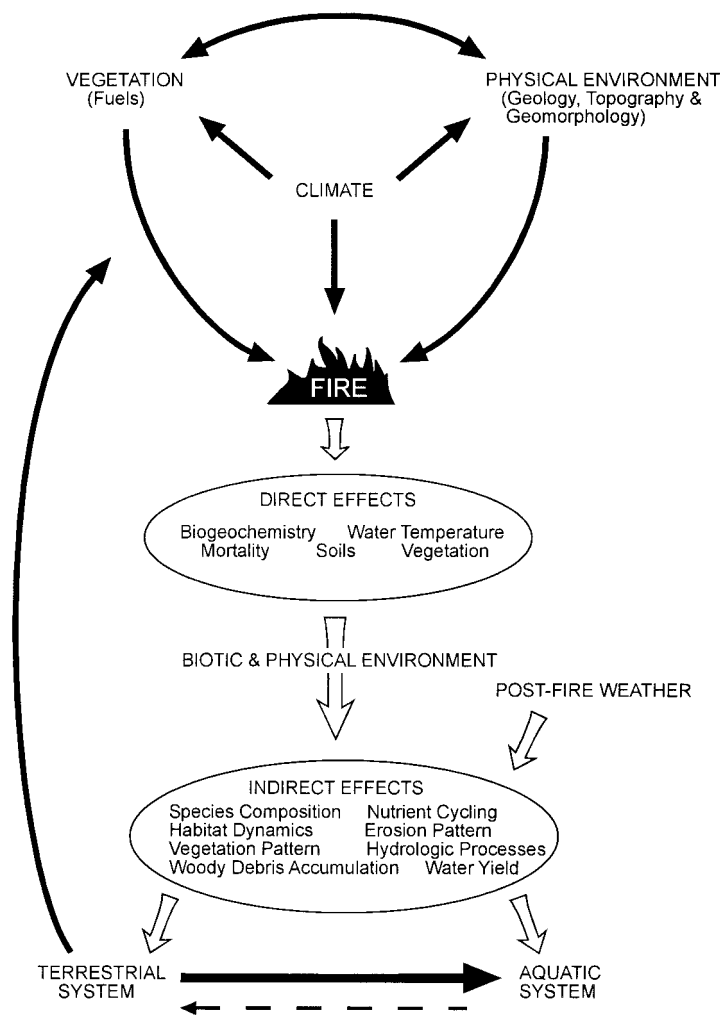
FIGURE 1.—Factors influencing fire and the effects of fire on terrestrial and aquatic ecosystems.

grated into these streams soon after the fire. Bull trout *Salvelinus confluentus* and rainbow trout (or more specifically, Columbia River redband trout *Oncorhynchus mykiss gairdneri*[1]) were apparently extirpated from sections of the Boise River basin during fires in 1992, but by 1995, fish densities were greater in the burned sections than in similar sections that did not burn (Rieman et al. 1997a).

The cause of fire-related fish mortalities has not often been established, but fatalities are generally associated with more intense and severe fires (Minshall et al. 1989; McMahon and deCalesta 1990; Rieman et al. 1997a). In some cases, water tem-

perature apparently reached lethal levels (Table 2). Nevertheless, Minshall and Brock (1991) doubted that temperatures in third-order streams reached levels that were lethal to fish.

Minshall et al. (1989) speculated that chemical toxicity from smoke or ash would cause fish mortality in second- and third-order streams (Table 3). During an experimental burn bordering a small stream in Washington, "distress" among yearling rainbow trout *O. mykiss* and several species of native fishes and mortality of native chinook salmon *O. tshawytscha* were attributed to fire-induced changes in stream pH (Cushing and Olson 1963). Although laboratory experiments with ash leachates failed to yield acute toxic effects after the Yellowstone fires in 1988, levels of trace elements

[1] The common and scientific names are those of Behnke (1992).

TABLE 1.—Selected references where a biological response to fire in forested watersheds was investigated in fluvial systems; NA means not available.

Source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
		Response by macroinvertebrates			
Lotspeich et al. (1970)	101,000 ha[c] (wf)	4 streams (9 sites)	1 year	Dennison River, AK	No statistically significant change detected in benthic aquatic fauna attributed to effects of fire
Stefan (1977)	1,100 ha (wf)	1 stream (order 3; 22 sites)	1 year	White Cap Wilderness, ID	Numbers of Plecoptera varied on artificial substrates among above-burn, burn, and below-burn sites; above-burn site adjacent to the burn had higher amounts of chlorophyll on periphyton samplers
Albin (1979)	200 ha (wf)	2 streams (order 1–2)	3 months	Yellowstone NP	Benthic insects abundant during and after fire, and no dead insects observed
Albin (1979)	481–506 ha (3 wf)	2 streams (2,120–3,930 ha) (7 sites)	35 years	Yellowstone NP	Greater abundance and diversity in burned watershed 35 years following fire
La Point et al. (1983)	26,000 ha (wf)	11 streams (290–29,880 ha) (order 1–5)	3 years	Middle Fork Salmon River, ID	Episodic storm events influenced composition of resident macroinvertebrate fauna; taxonomic richness, evenness, and diversity declined in burned watersheds; dominate functional feeding group was different in the burned watersheds
Roby (1989)	800 ha (wf)	2 streams (825 ha) (6 sites)	9 years	Plumas National Forest, CA	Increase in density and decrease in diversity 1 year postfire; differences with unburned control stream remained after 9 years; four other watersheds showed similar patterns up to 23 years following fire
Minshall et al. (1990)	26,000 ha (wf)	1 stream (10,900 ha) (order 4–5; 2 sites)	10 years	Middle Fork Salmon River, ID	Increase in abundance 1 year postfire
Jones et al. (1993)	322,000 ha (wf)	6 streams (25,000–116,000 ha) (order 4–6)	3 years	Yellowstone NP	Macroinvertebrate abundance, species richness, and diversity increased except in the Gibbon and Madison rivers where abundance, biomass, and richness declined somewhat; shift toward groups that utilize autochthonous food sources
Lawrence and Minshall (1994)	>200,000 ha (wf)	22 streams (order 1–4; 22 sites)	2 years	Yellowstone NP	Fire severity and distance of burn from channel were correlated with macroinvertebrate species diversity; streams with greatest disturbance had lowered diversity, but after 2 years these streams had higher macroinvertebrate diversity

TABLE 1.—Continued.

Source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Mihuc et al. (1996)	292,000 ha[d] (wf)	5 streams (140–26,800 ha) (order 1–4; 10 sites)	4 years	Yellowstone NP	Physical changes in stream habitat and alteration of resource availability were the primary factors affecting the postfire response of individual taxa
Minshall et al. (1997)	292,000 ha[d] (wf)	20 streams (140–18,000 ha) (order 1–4; 20 sites)	5 years	Yellowstone NP	Species appeared to respond individualistically; species with relatively short generation times and that disperse through drift appeared to be favored following fire
			Response by fishes		
Cushing and Olson (1963)	165 m section (eb)	1 stream (1 site)	30 min	Hanford Reservation, WA	Mortality of native chinook salmon *Oncorhynchus tshawytscha* in stream and distress of yearling rainbow trout *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) held in live-boxes attributed to pH change
Hall and Lantz (1969)	71 ha (sb)	1 stream (71 ha)	Immediate	Coast Range, OR	Mortality of juvenile coho salmon *Oncorhynchus kisutch,* coastal cutthroat trout *Oncorhynchus clarki clarki,* and sculpins *Cottus* spp. in a confined area of intense burn
Albin (1979)	200 ha (wf)	2 streams (order 1–2)	3 months	Yellowstone NP	Eggs of Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (formerly *Salmo clarki lewisi*) appeared normal during fire; fry emerged in both streams and appeared normal 2 months following fire
Albin (1979)	481–506 ha (2 wf)	2 streams (2,120–3,930 ha) (7 sites)	35 years	Yellowstone NP	Yellowstone cutthroat trout fry appeared to emerge from gravel earlier in burned watershed; egg incubation time estimated to be 4 d shorter than in unburned watershed
Jones et al. (1989)	292,000 ha[d] (wf)	1 stream (3 sites)	2 weeks	Yellowstone NP	Observed 45 dead fish (39 Yellowstone cutthroat trout and 6 unidentified) following accidental application of fire retardant directly to a section of stream
Norris and Webb (1989)	(eb)	5 streams (5 sites)	1 year	OR, ID, and CA	No mortality was observed in experiments where low concentrations fire retardant were directly applied to study sites
Woodward (1989)	526,000 ha[c] (wf)	4 streams (laboratory experiments)	3 weeks	Yellowstone NP	No mortality of Yellowstone cutthroat trout held in ash extracts; growth of juveniles retarded in 100% ash extracts

TABLE 1.—Continued.

Source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Gould (circa 1990)	292,000 ha[d] (wf)	1 stream (order 4; 1 site)	NA	Yellowstone NP	Interannual fluctuations of Yellowstone cutthroat trout abundance within normal range of variation
Novak and White (1990)	4,800 ha (wf)	1 stream (18,716 ha)	2 years	Missouri River Basin, MT	Biomass of brown trout *Salmo trutta* and rainbow trout decreased 98% in the year following a fire-related debris torrent; within 2 years numbers and biomass of rainbow trout exceeded prefire estimates; brown trout numbers remained low because of poor access for recolonization
Jones et al. (1993)	322,000 ha (wf)	6 streams (25,200–116,500 ha) (order 4–6)	3 years	Yellowstone NP	No fire-related changes observed in growth or abundance of fish in study rivers; some dead fish found in smaller streams immediately following fire, but populations were reestablished within 1 year postfire
Bozek and Young (1994)	562,000 ha (wf)	2 streams (4,946–6,423 ha)	2 years	North Fork Shoshone River, WY	Fish mortalities (1 rainbow trout, 4 Yellowstone cutthroat trout, 11 brook trout *Salvelinus fontinalis,* and 2 Yellowstone cutthroat trout × rainbow trout hybrids) associated with debris torrent 2 years after fire burned the watershed
Rinne (1996)	12,000 ha (wf)	3 streams (order 1)	3 years	Tonto National Forest, AZ	Two populations of brook trout and one population of rainbow trout effectively extirpated following fire-related debris torrents
Minshall et al. (1997)	292,000 ha[d] (wf)	20 streams (140–18,000 ha) (order 1–4; 20 sites)	5 years	Yellowstone NP	Up to 10 dead Yellowstone cutthroat trout/250 m of stream immediately following fires in two third-order streams
Rieman et al. (1997)	105,000 ha (wf)	3 streams (5,800–11,500 ha) (9 sites)	4 years	Boise River Basin, ID	Extirpation of redband trout *Oncorhynchus mykiss* and bull trout *Salvelinus confluentus* from some reaches; densities exceed prefire estimates in 2 years

[a] Fire types: eb = experimental burn; sb = slash burn; wf = wildfire.
[b] Location abbreviations: AK = Alaska; AZ = Arizona; CA = California; ID = Idaho; MT = Montana; NP = National Park; OR = Oregon; WA = Washington; WY = Wyoming.
[c] Areal estimates changed from acres to hectares.
[d] Areal estimate from Turner and Romme (1994).

(e.g., aluminum, iron, lead, and zinc) in the ash extracts were above levels considered safe for aquatic organisms (Woodward 1989).

Analysis of data collected during an intense fire in northwestern Montana in 1988 revealed potential mechanisms for the increase of chemical concentrations in streams to lethal levels (Table 3).

Spencer and Hauer (1991) reported that ammonium concentrations increased more than 40-fold over background levels, and although concentrations fluctuated widely, they did not decline to background levels until the fire was extinguished by rain (approximately 6 weeks later). Dissolved phosphorus also increased dramatically within 24

h of the fire, but within 2 weeks, phosphorus concentrations returned to background levels. Laboratory studies suggested that adsorption of smoke gases into surface waters explained the increase in ammonium; phosphorus increases were attributed to leaching of aerially deposited ash (Spencer and Hauer 1991).

Another source of fish mortality is associated with the use of fire retardant (Van Meter and Hardy 1975). Dead fish have been reported following fire retardant application (Jones et al. 1989), but documentation is poor (Norris and Webb 1989). In cases where mortality was alleged (i.e., cause of death was unsubstantiated), toxic effects were apparently temporary (Hakala et al. 1971; Jones et al. 1989; Norris and Webb 1989).

Indirect Physical Effects

Hydrologic processes.—Most temporally intermediate effects of fire on aquatic systems are related to hydrologic change from increased water yield and sediment routing (Table 2). Soil properties (e.g., water repellency, porosity, structure, texture, and temperature) and erosion processes (e.g., surface erosion, mass wasting, and channel erosion) are altered by fire (Klock and Helvey 1976; McNabb et al. 1989; White 1996). Hydrologic processes control channel morphology (Swanson 1981; Trush 1990; Meyer et al. 1995), sediment composition and concentration (Beaty 1994; White 1996; Minshall et al. 1997), and recruitment and distribution of large woody debris (Van Sickle and Gregory 1990; Young 1994; McIntyre and Minshall 1996). Therefore, the magnitude and scale of effects are related to the size and severity of fire; geology, topography, and size of the stream system; and amount, magnitude, and timing of postfire precipitation events (Swanson 1981; Meyer et al. 1992; Meyer et al. 1995). Erosional effects are most extreme where the majority of vegetation and duff has been consumed by fire, soils are highly erosive, and large precipitation events occur soon after the fire. Areas where a large proportion of the drainage is burned in a single event are most susceptible to erosional processes. Mass wasting and channel alteration are generally greatest in the first 10 years after a fire (Swanson 1981; McNabb and Swanson 1990; Swanston 1991).

Some postfire erosion events may appear catastrophic, but these events are important in maintaining long-term habitat complexity and suitable spawning and rearing areas in some systems (Everest et al. 1987; Reeves et al. 1995). Furthermore,

native fishes have developed a complex variety of life history strategies that increase the probability of persistence during periods of environmental fluctuation (Warren and Liss 1980; Sedell et al. 1990; Rieman et al. 1997a). Even in cases where fish are extirpated (see *Biological Effects,* below), reinvasion is rapid (i.e., <2 years) if habitat connectivity is maintained (Novak and White 1990; Rieman and Clayton 1997; Rieman et al. 1997a).

Swanson (1981) developed a fire index, based on fire intensity, frequency, and areal extent, and a geomorphic index, based on hillslope gradient and the effectiveness of vegetation in regulating sediment movement, to estimate the fire-induced proportion of total sediment yield for five landscape–ecosystem types (Figure 2). Results suggested that in highly erosive landscapes with frequent fires of high intensity (e.g., steepland chaparral), more than 70% of the long-term sediment yield occurred during and immediately following fires. Fire-induced sediment yields for most ecosystem types were much lower, however, and in highly unstable portions of the Cascade Range, only about 30% of the total sediment yield was attributable to fires. Similarly, there is evidence that forest fires have influenced sedimentation in some portions of Yellowstone National Park throughout the Holocene (Meyer et al. 1992, 1995), and Meyer (1993) reported that approximately one-third of the total thickness of 29 stratigraphic sections from alluvial fans in erosive watersheds were the result of fire-related debris flows and deposits. In less erosive regions (Laurentian upland forests), areas with a low fire index (steep Appalachian Mountain hardwood forest), and areas with both low geomorphic sensitivity and a low fire index (alluvial flat forests), the proportion of fire-induced sediment yields dropped to approximately 5% (Swanson 1981).

Although physical changes to stream channels are common in the first 1–4 years following a fire (Minshall et al. 1990; Swanston 1991; Minshall et al. 1997), effects on woody debris recruitment can last for decades in forested drainages (Table 2). Presence of large wood in streams is important because it controls channel morphology, and sediment and water routing (Harmon et al. 1986; Everest et al. 1987; Trotter 1990). After wildfires, large wood may persist in stream channels through the period of forest reestablishment (Swanson and Lienkaemper 1978). As a consequence, the rate of pool formation usually increases, and habitat structure may be altered to the benefit of fishes (Swanson and Lienkaemper 1978; Sedell and

TABLE 2.—Selected references where physical response to fire in forested watersheds was investigated in fluvial systems; NA means not available.

Response and source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Hydrologic responses					
Channel morphology					
La Point et al. (1983)	26,000 ha (wf)	11 streams (290–29,880 ha) (order 1–5)	3 years	Middle Fork Salmon River, ID	Episodic storm events influence stream substrate
Roby (1989)	800 ha (wf)	1 stream (825 ha)	6 years	Plumas National Forest, CA	Channel cross sections revealed slight widening 1 year postfire; substantial widening and deepening 3 years postfire; channel profile was similar to prefire after 6 years
Minshall et al. (1990)	26,000 ha (wf)	1 stream (10,900 ha) (order 4–5; 2 sites)	10 years	Middle Fork Salmon River, ID	Channel alterations continuing after 10 years
Jones et al. (1993)	322,000 ha (wf)	6 streams (25,200–116,500 ha) (order 4–6)	3 years	Yellowstone NP	Little change in channel morphology; stream banks remained stable
Bozeck and Young (1994)	562,000 ha (wf)	2 streams (4,946–6,423 ha)	2 years	North Fork Shoshone River, WY	Channel alterations caused by debris and mud jams
Meyer et al. (1995)	292,000 ha[c] (wf)	3 streams (25,600–75,200 ha) (order 4–5)	Long-term	Yellowstone NP	Relatively minor climate changes during the late Holocene have had significant affects on fire regime and alluvial processes in the study streams
Minshall et al. (1997)	292,000 ha[c] (wf)	20 streams (140–18,000) (order 1–4; 20 sites)	5 years	Yellowstone NP	Cutting and filling related to postfire runoff events greatest in higher gradient streams
Erosion					
Lotspeich et al. (1970)	101,000 ha[d] (wf)	4 streams (9 sites)	1 year	Dennison River, AK	Only evidence of increased erosion was in fire trails
DeByle and Packer (1972)	65 plots, 4–23 ha[d] (sb)	2 streams (24 plots)	7 years	Western Montana	Increased erosion related to localized intense summer precipitation events; greatest for 2 years following logging and burning; roads and firebreaks had much greater potential of producing overland flow
Helvey (1980)	48,600 ha[d] (wf)	3 streams (473–564 ha[c])	9 years	Entiat Experimental Forest, WA	Postfire increases in erosion; results affected by salvage logging
White (1996)	Unknown (wf)	7 basins (0.1–0.41 ha)	15 years	Bandelier National Monument, NM	Increased erosion 3 years postfire; sediment delivery ceased in most basins 15 years postfire
Organic matter					
McIntyre and Minshall (1996)	400,000 ha (wf)	5 streams (200–1,090 ha) (order 1; 5 sites)	2 years	Yellowstone NP	Short-term reduction in coarse particulate organic matter in streams of burned watersheds

Table 2.—Continued.

Response and source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Sedimentation					
Helvey (1980)	48,600 ha[d] (wf)	3 streams (473–564 ha[c])	9 years	Entiat Experimental Forest, WA	Postfire increases in sedimentation; results affected by salvage logging; debris torrents occurred in association with intense rainstorms
Swanson (1981)	NA	NA	NA	North America	Fire-related sediment yield determined by fire regime and geomorphic sensitivity
Meyer et al. (1992)	292,000 ha[c] (wf)	2 streams (25,600–57,000 ha) (order 4–5)	Long-term	Yellowstone NP	Fire-related sedimentation was most active during centennial-scale drought-dominated periods
Beaty (1994)	NA (wf)	1 stream (170 ha; order 2)	8 years	Experimental Lakes Area, ON	Bedload increased 20-fold initially; recovery in 5–6 years; particle size increased with time; effects following a second fire (6 years after the first) were not as great and were short-lived
Meyer et al. (1995)	292,000 ha[c] (wf)	3 streams (25,600–75,200 ha) (order 4–5)	Long-term	Yellowstone NP	In one watershed, 30% of late Holocene fan alluvium was fire related
Troendle and Bevenger (1996)	48,000 ha (wf)	2 streams (4,950–6,680 ha)	3 years	North Fork Shosone River, WY	Sediment concentration and total suspended load increased in burned watershed
Minshall et al. (1997)	292,000 ha[c] (wf)	20 streams (140–18,000 ha) (order 1–4; 20 sites)	5 years	Yellowstone NP	Increased substrate embeddedness
Water yield					
Helvey (1972)	48,600 ha[d] (wf)	3 streams (473–564 ha[c])	1 year	Entiat Experimental Forest, WA	Yield increase due to loss of riparian vegetation
Albin (1979)	481–506 ha (2 wf)	2 streams (2,120–3,930 ha) (7 sites)	35 years	Yellowstone NP	Increased yield and greater seasonal fluctuation in burned watershed
Helvey (1980)	48,600 ha[d] (wf)	1 stream (564 ha[c])	9 years	Entiat Experimental Forest, WA	Increased yields for 7 years
Schindler et al. (1980)	1,457 ha (wf)	2 streams (63–170 ha)	6 years	Experimental Lakes Area, ON	Increased yields for 3 years
Tarapchak and Wright (1986)	5,900 ha (wf)	(29–40 ha)	2 years	Boundary Waters Canoe Area, MN	Increase in discharge of tributary streams
Stottlemyer (1987)	4,200 ha (wf)	1 stream (3,535 ha) (order 2–3; 4 sites)	3 years	Heart Lake, Yellowstone NP	Pronounced increase in discharge of streams
Troendle and Bevenger (1996)	48,000 ha (wf)	2 streams (4,950–6,680 ha)	3 years	North Fork Shosone River, WY	Yield increased in burned watershed
Woody debris					
Swanson and Lienkaemper (1978)	NA	4 streams	Long-term	Cascade Range, OR	Dominance of prefire and postfire woody debris in streams gradually changed through time
Minshall et al. (1990)	26,000 ha (wf)	1 stream (10,900 ha) (order 4–5; 2 sites)	10 years	Middle Fork Salmon River, ID	Initial decrease in woody debris; down trees appearing by year 4; debris jams by year 10
Young (1994)	48,000 ha (wf)	2 streams (4,950–6,680 ha)	2 years	North Fork Shoshone River, WY	Woody debris transport increased in burned watershed after fire

TABLE 2.—Continued.

Response and source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Reeves et al. (1995)	NA (wf)	3 streams (1,400–1,800 ha)	Long-term	Coast Range, OR	Woody debris increased with time since disturbance (90 to >350 years)
Minshall et al. (1997)	292,000 ha[c] (wf)	20 streams (140–18,000 ha) (order 1–4; 20 sites)	5 years	Yellowstone NP	More woody debris at burned sites than reference sites; retention dynamics were altered at burned sites
Hydrophobicity McNabb et al. (1989)	NA (sb)	8 plots (0.25 ha each)	5 months	Siskiyou Range, OR	Water repellency increased, and infiltration rate decreased; changes were neither large or long lasting

Nonhydrologic physical responses

Response and source	Fire size (type)[a]	Spatial scale	Time scale	Location[b]	Comments
Water temperature Cushing and Olson (1963)	165 m section (eb)	1 stream (1 site)	30 min	Hanford Reservation, WA	Rapid temperature increase; observed fish mortalities attributed pH change
Hall and Lantz (1969)	71 ha (sb)	1 stream (71 ha)	During fire	Coast Range, OR	Rapid increase from 13–28°C; fish mortalities where fire was most intense
Helvey (1972)	48,600 ha[d] (wf)	3 streams (473–564 ha[c])	1 year	Entiat Experimental Forest, WA	Water temperature increased (up to 5.5°C) during summer; no detectable change during winter
Helvey et al. (1976)	48,600 ha[d] (wf)	3 streams (473–564 ha[c])	3 years	Entiat Experimental Forest, WA	Water temperature increased (up to 5.5°C) with increased insolation but never exceeded 16.7°C
Albin (1979)	200 ha (wf)	2 streams (order 1–2)	3 months	Yellowstone NP	Highest temperature recorded in streams during or after the fire was 12°C
Albin (1979)	481–506 ha (2 wf)	2 streams (2,120–3,930 ha) (7 sites)	35 years	Yellowstone NP	Summer water temperatures averaged approximately 1.5°C higher in burned watershed
Feller (1981)	NA (sb)	1 stream	13 hours	British Columbia	Water temperature increased from 3.3°C within 6 h of a slash burn; after 13 h, water temperatures had returned to near prefire levels
Amaranthus et al. (1989)	40,000 ha (wf)	3 streams (order 1)	1 year	Grants Pass, OR	Increased direct insolation and water temperature; change negligible downstream
Minshall et al. (1997)	292,000 ha[c] (wf)	20 streams (140–18,000 ha) (order 1–4; 20 sites)	5 years	Yellowstone NP	Maximum water temperatures were higher at burned sites (often >20°C) than reference sites

[a] Fire types: eb = experimental burn; sb = slash burn; wf = wildfire.
[b] Location abbreviations: AK = Alaska; CA = California; ID = Idaho; MN = Minnesota; NM = New Mexico; NP = National Park; ON = Ontario; OR = Oregon; WA = Washington; WY = Wyoming.
[c] Areal estimate from Turner and Romme (1994).
[d] Areal estimates changed from acres to hectares.

Dahm 1984; Minshall et al. 1997). Accumulation of coarse wood is important to decomposers and detritus feeders, but excessive abundance can block fish passage, cover important spawning sites, and damage habitat during postfire flood events (Swanston 1991). Over longer periods of time, however, benefits of fire-related debris recruitment probably outweigh the negative effects (Swanson et al. 1982; Reeves et al. 1995).

Anthropogenic activities can exacerbate the effects of natural events such as fire. In many cases, erosion at a watershed scale is more closely linked to timber harvest and road construction than fire (Brown and Krygier 1971; Swanston 1971; Swanston and Swanson 1976). For instance, less than 1% of an estimated total annual sediment yield for the South Fork Salmon River (Idaho) was due to fire; roads were responsible for 85% of the total annual sediment budget (Nobel and Lundeen 1971). Marston and Haire (1990) reported that following the fires in the Greater Yellowstone Ecosystem in 1988, surface erosion was greatest at sites outside the national park that were logged before burning. Erosional effects generally peak within 10 years following a fire event (McNabb and Swanson 1990; White 1996), but road building, log yarding, tree clearing, and slash burning may produce a press disturbance with erosion that can persist for decades (Swanston 1971; Yount and Niemi 1990; Frissell et al. 1997).

Water temperature.—Another important physical effect of fire is elevated water temperature resulting from the reduction in streamside vegetation and associated increases in insolation (Table 2). In the year following a wildfire in north-central Washington, maximum daily water temperatures were 5.6°C above temperatures predicted for unburned conditions (Helvey 1972). Amaranthus et al. (1989) reported that maximum water temperature increased 3.3–10.0°C at intensively burned sites 1 year after a fire in portions of three headwater drainages in southwestern Oregon. Albin (1979) found that elevated water temperatures may persist for decades; however, increased discharge associated with reduced evapotranspiration can have a secondary, but compensatory, influence on water temperature (Helvey et al. 1976). There is some evidence that even when water temperature increases are great at sites in headwater streams, changes may be negligible downstream. For instance, Amaranthus et al. (1989) reported that water temperature did not increase appreciably at the mouth of tributaries draining an area where 5% of the headwater watershed burned.

Although water temperature of streams may increase after streamside vegetation is removed (Gray and Edington 1969), predicting the biological consequences is difficult (Beschta et al. 1987). Effects depend on the burn intensity, spatial pattern of the burn, stream size, stream network complexity, watershed topography, normal temperature ranges of affected stream reaches, and life history stage of the organisms present at the time of the fire. For instance, elevated temperatures may alter abundance, species diversity, egg incubation, and offspring survival (Beschta et al. 1987; Reeves et al. 1993). In areas where low water temperatures limit primary production, elevated water temperatures (nonlethal) following canopy burning may actually increase productivity (Albin 1979; Minshall et al. 1989).

Indirect Chemical Effects

Fluvial systems.—The level of nutrient input to aquatic systems following fire is contingent upon factors such as fire intensity and size, short- and long-term weather patterns, and the physical, chemical, and biological characteristics of the watershed (Table 3). As a result, effects of fire on water chemistry vary substantially among study areas (Tiedemann et al. 1979; Beschta 1990). Nevertheless, some generalizations are possible.

The presence of chemical constituents in smoke and ash can have a substantial influence on stream water chemistry until the fire is extinguished. Clayton (1976) reported that concentrations of calcium, magnesium, potassium, sodium, and total nitrogen in precipitation that fell during periods of high smoke in Idaho were 20–70 times greater than concentrations in precipitation collected during nonfire periods. As noted previously, experimental work of Spencer and Hauer (1991) linked influxes of ammonium to diffusion of nitrogen volatilized in smoke gases and peaks of phosphorus to leachate from ash deposited directly into streams. Although Johnson and Needham (1966) did not observe a measurable change in ion concentrations for 2 years after a fire in Sagehen Creek, California, their data suggest a distinct pulse of ions (except sodium) while the fire was still smoldering and before postfire precipitation.

Immediately after a fire, streams adjacent to burned areas often exhibit peak concentrations of nitrogen and phosphorus that generally last no more than a few weeks (Fredriksen 1971; Brown et al. 1973). Such pulses are commonly associated with initial postfire precipitation (e.g., Albin 1979), but Beschta (1990) suggested that infre-

TABLE 3.—Selected studies where chemical response to fire in forested watersheds was investigated in fluvial systems; NA means not available.

Source	Fire size (type)[a]	Spatial size[a]	Time scale	Location[b]	Comments
Cushing and Olson (1963)	165 m section (eb)	1 stream (1 site)	30 min	Hanford Reservation, WA	Increase in ions attributed to ash deposit; rapid increase in pH
Johnson and Needham (1966)	NA (wf)	1 stream (4,921 ha)	2 years	Tahoe National Forest, CA	No observed effect of fire on ionic composition of stream water
Lotspeich et al. (1970)	101,000 ha[c] (wf)	4 streams (9 sites)	1 year	Dennison River, AK	Increased K and chemical oxygen demand in streams draining burned areas
Fredriksen (1971)	NA (sb)	3 streams (3 sites)	3 years	H. J. Andrews Experimental Forest, OR	Following slash burning, NH_4 and Mn concentrations exceeded Federal Water Pollution Control Standards for 12 d; cations increased 1.6–3.0 times in burned drainage; pH increased
DeByle and Packer (1972)	65 plots 4–23 ha[d] (sb)	2 watersheds (24 plots)	7 years	Western Montana	Increase of N, P, K, Ca, Mg, and Na in surface runoff following fire; return to preburn levels in 2–4 years; high among-site variability
Brown et al. (1973)	70–300 ha (sb)	3 streams (71–300 ha)	6 years	Oregon Coast Range	Potassium increased in watershed that was clearcut and burned; returned to prelogging levels within 2 months; NO_3 increased and returned to prelogging levels 6 years postfire
Clayton (1976)	900 ha (wf)	1 stream (5 gages)	3 months	South-Central Idaho	Concentrations of Na, K, Ca, and N in precipitation falling through smoke were 20–70 times greater than in normal precipitation
Helvey et al. (1976)	48,600 ha[d] (wf)	1 stream (473 ha[d])	3 years	Entiat Experimental Forest, WA	Nitrate concentrations increased during spring runoff for 2 years postfire in an unfertilized watershed; cation losses (from concentration and discharge data) doubled during the same period
Albin (1979)	200 ha (wf)	2 streams (order 1–2)	3 months	Yellowstone NP	Significant increase in ions associated with ash leaching during initial postfire rain event
Albin (1979)	481–506 ha (2 wf)	2 streams (2,120–3,930 ha) (7 sites)	35 years	Yellowstone NP	Water quality similar between burned and unburned watersheds, but higher water yield and mineral export in burned watershed
Schindler et al. (1980)	1,457 ha (wf)	2 streams (63–170 ha)	6 years	Experimental Lakes Area, ON	Increased concentrations and yields of N, P, and K during 3 postfire years
La Point et al. (1983)	26,000 ha (wf)	11 streams (290–29,880 ha) (order 1–5)	3 years	Middle Fork Salmon River, ID	Concentration of F and PO_4 and yield of Ca, alkalinity, Cl, and PO_4 significantly greater in burned watershed

TABLE 3.—Continued.

Source	Fire size (type)[a]	Spatial size[a]	Time scale	Location[b]	Comments
Woodward (1989)	526,000 ha[c] (wf, lab)	4 streams (lab)	7 months	Yellowstone NP	High levels of trace elements in many samples, but no acute toxic effects to fish in laboratory tests
Spencer and Hauer (1991)	15,500 ha (wf, lab)	2 streams (order 3)	6 weeks	Northwest Montana	Total N and P increased 40-fold over reference values; diffusion of smoke gases in stream water was source of N; P source was from leaching of ash deposited in streams
Bayley et al. (1992)	NA (sb, wf)	3 streams (12–170 ha)	18 years	Experimental Lakes Area, ON	Watershed type and fire intensity directly related to N and P inputs to aquatic systems
Jones et al. (1993)	322,000 ha (wf)	6 streams (25,200–116,500 ha) (order 4–6)	3 years	Yellowstone NP	Postfire samples within range of prefire water chemistry data (except Si in Madison River)
Brass et al. (1996)	292,000 ha[c] (wf)	6 streams (6 sites)	5 years	Yellowstone NP	Nitrates increased 2.6–33 times for 5 years postfire; PO_4 2.0–29 times greater for 5 years postfire
Robinson and Minshall (1996)	292,000 ha[c] (wf)	20 streams (140–18,000 ha) (order 1–4; 21 sites)	5 years	Yellowstone NP	Nitrates concentrations 3–4 times greater at burn sties with moderate and high amounts of physical change; NO_3 concentration directly related to the proportion of catchment burned

[a] Fire types: sb = slash burn; wf = wildfire; lab is laboratory experiments.

[b] Location abbreviations: AK = Alaska; CA = California; ID = Idaho; NP = National Park; ON = Ontario; OR = Oregon; WA = Washington.

[c] Areal estimates changed from acres to hectares.

[d] Areal estimate from Turner and Romme (1994).

quent sampling, rapid uptake by stream biota, and sediment adsorption may sometimes inhibit detection of these nutrient peaks. Although logging (without slash burning) may lead to increased chemical concentrations in aquatic systems for extended periods, rapid nutrient peaks coinciding with timber removal have not been documented (Fredriksen 1971; Bayley et al. 1992).

Chemical constituents in streams may remain elevated for years because the loss of vegetation following fire can interrupt the cycling of nutrients in a forest ecosystem, and subsequently, exports to aquatic systems are increased (Wright 1976; Bayley et al. 1992). Elevated concentrations of chemical constituents in streams have been described after wildfires (Lotspeich et al. 1970; La Point et al. 1983; Brass et al. 1996; Robinson and Minshall 1996) and after slash burning of logging debris (Fredriksen 1971; DeByle and Packer 1972; Brown et al. 1973). Similarly, wind damage in forests may yield nutrient losses analogous to those observed after forest fires (Schindler et al. 1980).

Fredriksen (1971) reported that elevated temperature and water content in soils stimulate microorganisms, increasing postfire litter decomposition. As respiration rises, bicarbonate anion levels increase concomitantly with leaching of cations from the system (Fredriksen 1971). Mineralized forms of plant nutrients converted to ash during burning become more soluble. When water contacts the ash, solutes are leached into the soil or carried away with runoff (DeByle and Packer 1972). Stottlemyer (1987) suggested that above certain precipitation thresholds, ion conservation mechanisms fail, resulting in disproportionately high ion discharges in some tributary basins; however, at the watershed scale, chemical constituents are often conserved. In some cases soil retention of nutrients leached from ash may be high (Grier
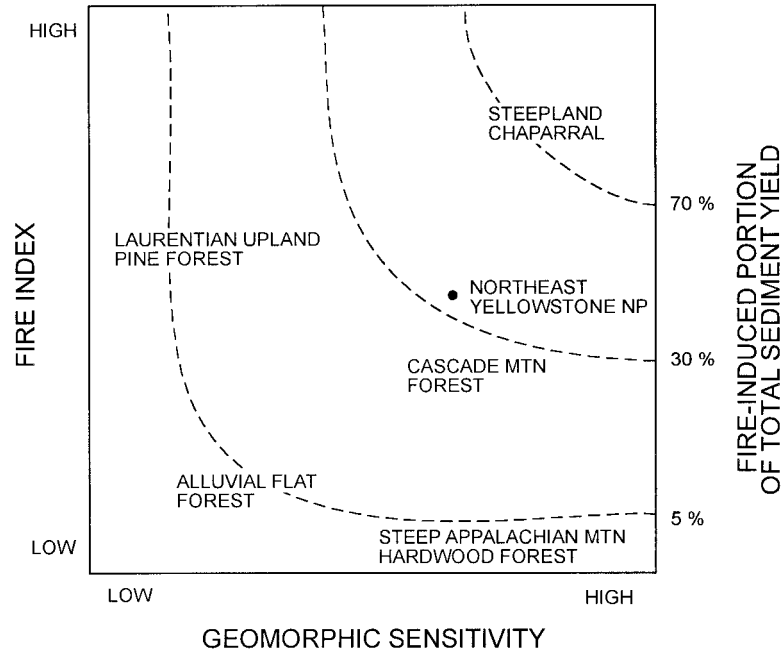
FIGURE 2.—Hypothetical distribution of selected landscape ecosystem types in relation to geomorphic sensitivity (erosion and sedimentation), fire frequency and intensity, and proportion of total sediment yield that can be attributed to fire (adapted from Swanson 1981). Abbreviations are MTN (mountain) and NP (National Park).

1975), but variation among sample sites and among years is often substantial (Lotspeich et al. 1970; DeByle and Packer 1972). As vegetation becomes reestablished, fewer nutrients are available for leaching, soil erosion diminishes (McColl and Grigal 1975; Uhl and Jordan 1984), and chemical constituents in streams generally decrease to levels observed before the fire.

Nitrate-nitrogen is one of the most mobile chemical components of soil–water systems, and in streams, postfire increases of nitrates exceed other chemical changes (Tiedemann et al. 1979; Minshall et al. 1997). If mineral nitrogen released by decomposition of organic nitrogen is not sequestered by plants or microorganisms, nitrogen loss as nitrate may occur (Fredriksen 1971). Nitrate loss is especially noticeable following an intense fire when the amount of burned biomass is high and density of microorganisms is reduced substantially (Stottlemyer 1987; Brass et al. 1996; Minshall et al. 1997). Following the 1988 fires in Yellowstone National Park, for example, nitrate concentration was the only variable that increased substantially in burned catchments, and in streams with moderate to high amounts of physical change, nitrate values increased to 3–4 times initial levels (Robinson and Minshall 1996). Elevated levels of

nitrate-nitrogen in streams have been reported 5 years or more after a fire (Brown et al. 1973; Bayley et al. 1992; Brass et al. 1996).

Although nutrient influxes to aquatic systems are sometimes high, many of the nutrients in a forested ecosystem may be retained on-site even after a major fire (DeByle and Packer 1972; Wright 1976; Bayley et al. 1992). Following a 125,000-ha stand-replacement fire in Alaska (1966), Lotspeich et al. (1970) found increases in soluble total organic carbon, calcium, magnesium, and potassium in the organic soil layer; however, only chemical oxygen demand and potassium increased in stream samples collected for the first 2 years after the fire. In five drainages (fifth and sixth order) in Yellowstone National Park, Jones et al. (1993) found that the only change in water chemistry attributable to the 1988 fires was increased silica concentration in the Gibbon and Madison rivers.

Lacustrine systems.—Effects of fire on nutrient levels in lacustrine systems are less well documented (Table 4). An exception is a group of studies following a fire in the Boundary Waters Canoe Area in northeastern Minnesota that burned over half of the overstory vegetation in the watersheds of two lakes (Wright 1976; McColl and Grigal 1977; Tarapchak and Wright 1986). Despite ob-

TABLE 4.—Selected studies where physical, chemical, and biological responses to fire in forested watersheds were investigated in lacustrine systems; NA means not available.

Response and source	Fire size (type)[a]	Number of lakes (surface area)	Time scale	Location[b]	Comments
Sedimentation					
Lathrop et al. (1994)	292,000 ha[c] (wf)	4 lakes (11,000–34,000 ha)	6 years	Greater Yellowstone Ecosystem	Postfire increase (2 years) in suspended sediment in the Snake River flowing into Jackson Lake (WY), but no detectable effect on water quality in Yellowstone Lake
Chemical					
McColl and Grigal (1975)	6,000 ha (wf)	2 lakes (29–36 ha)	3 years	Boundary Waters Canoe Area, MN	Increase in overland flow and soil water concentrations of P for 2 years; no significant effect on lakes and tributaries
McColl and Grigal (1977)	6,000 ha (wf)	3 lakes (29–40 ha)	3 years	Boundary Waters Canoe Area, MN	Burning had little effect on chemical characteristics of the aquatic systems when compared to effects on watershed soils
Wright (1976)	5,900 ha (wf)	3 lakes (29–40 ha)	2 years	Boundary Waters Canoe Area, MN	Increases in K and P in tributaries, but no evidence of increased loading in lakes
Jones et al. (1979)	1,236 ha (wf)	1 lake (34,000 ha)	3 years	Yellowstone Lake, Yellowstone NP	Increased levels of total dissolved solids and Si in the portion of the lake nearest the burn
Tarapchak and Wright (1986)	5,900 ha (wf)	3 lakes (29–40 ha)	2 years	Boundary Waters Canoe Area, MN	Major ions, Si, and TN and TP did not differ significantly among two burned drainages and control
Stottlemyer (1987)	4,200 ha (wf)	1 lake (870 ha[d])	3 years	Heart Lake, Yellowstone NP	Inputs of Ca, Mg, K, and NO_3 into the lake did not increase significantly following the fire
Lathrop (1994)	292,000 ha[c] (wf)	2 lakes (1,100–34,000 ha)	15 years	Yellowstone NP	Atmospheric deposition had greater influence on water chemistry than fire-mediated inputs from upland watersheds
Bayley et al. (1992)	NA (sb, wf)	NA	18 years	Experimental Lakes Area, ON	Minimal change in lake water quality because renewal time minimized effects of fire-related nutrient inputs from streams
Theriot et al. (1997)	292,000 ha[c] (wf)	1 lake (34,000 ha)	11 years	Yellowstone Lake, Yellowstone NP	No trends associated with fire; increases in Si due to reduced biological demand; NO_3 varied with winter precipitation
Biological					
Gresswell (unpublished)	292,000 ha[c] (wf)	1 lake (34,000 ha)	10 years	Yellowstone Lake, Yellowstone NP	No significant change in growth of Yellowstone cutthroat trout associated with fire
Bradbury (1986)	5,900 ha (wf)	2 lakes (29–36 ha)	80 years	Boundary Waters Canoe Area, MN	Paleolimnological study suggested no significant change in phytoplankton community attributable to fire
Tarapchak and Wright (1986)	5,900 ha (wf)	3 lakes (29–40 ha)	2 years	Boundary Waters Canoe Area, MN	No significant change in phytoplankton community attributable to fire

[a] Fire types: sb = slash burn; wf = wildfire.
[b] Location abbreviations: MN = Minnesota; NP = National Park; ON = Ontario.
[c] Areal estimate from Turner and Romme (1994).
[d] Areal estimate from Theriot et al. (1997).

served increases in nutrient export in tributary streams, Wright (1976) reported that precipitation falling directly on the lakes was the principal source for ions and phosphorus in the study lakes. In a separate study of this fire, McColl and Grigal (1975) concluded that very little of the phosphorus mobilized by the fire reached the lakes. Differences in soil type were apparently more important than fire in determining chemical characteristics of streams or lakes in these burned watersheds because most water enters these aquatic systems through subsurface flow (McColl and Grigal 1977).

Stottlemyer (1987) studied the nutrient levels in a large lake in Yellowstone National Park following a fire that burned 93% of a tributary drainage in 1979. Increases in chemical concentrations in the lake as a consequence of the fire were small, and variations in precipitation inputs was believed to be the source of the observed changes. Following wildfires that burned approximately 28% of the Yellowstone Lake watershed in 1988, dissolved silica was the only chemical constituent that exhibited changes that were not associated with annual fluctuations in precipitation (Lathrop 1994; Lathrop et al. 1994; Theriot et al. 1997). Increases in silica were also documented after a small fire burned several tributary drainages of the Southeast Arm of Yellowstone Lake in 1976 (Jones et al. 1979). Theriot et al. (1997) and Kilham et al. (1996) argued that increases in silica were due to a reduced biological demand because drought had reduced inputs of nitrogen and caused productivity to decline. Atmospheric inputs also appeared to dominate annual trends in water quality in Lewis Lake before and after the 1988 fires (Lathrop 1994; Theriot et al. 1997). Bayley et al. (1992) concluded that forest fires have little effect on the water quality of lakes because renewal times minimize the consequences of a few years of somewhat increased inputs of some nutrients.

Indirect Biological Effects

Fluvial systems: macroinvertebrates and periphyton.—Few studies before 1980 focused specifically on the fate of aquatic organisms following fire, but in the past two decades a substantial amount of new information has been reported on the biological effects of fire in aquatic systems, especially concerning macroinvertebrate communities (Table 1). Three years following a 26,000-ha fire in the Middle Fork of the Salmon River in Idaho, macroinvertebrate distribution in burned and unburned sites did not vary in conjunction with observed shifts in water chemistry, but some changes in functional feeding groups (Cummins 1978) were noted (La Point et al. 1983). Apparently the macroinvertebrate stream community was strongly influenced by substrate instability associated with channel erosion resulting from the interaction of postfire storm events and unstable slopes. Richards and Minshall (1992) reported that in the first 5 years following the fire, streams in the burned area exhibited more annual variation in macroinvertebrate diversity than reference streams, and although variation declined somewhat through time, species richness remained greater in reference streams than in streams from burned drainages. Minshall et al. (1990) suggested that as substrate stabilizes, productivity expands in response to increased light and temperature associated with the initial removal of riparian vegetation and subsequent successional change (Figure 3).

In the year following the 1988 fires in Yellowstone National Park, minor declines in periphyton biomass (Robinson et al. 1994a) and macroinvertebrate abundance, species richness, and diversity were noted (Lawrence and Minshall 1994; Minshall et al. 1995; Mihuc et al. 1996). By 1990, periphyton biomass and macroinvertebrate indices had increased, but erosional events associated with spring runoff and summer spates in 1991 and 1992 substantially altered the physical habitat of smaller study streams. Declines in periphyton biomass were greater in first- and second-order streams than in larger (third- and fourth-order) streams, and diatom diversity was directly related to the level of disturbance (Robinson et al. 1994a, 1994b). Macroinvertebrate abundance, species richness, and diversity also declined in smaller study streams during this period (Minshall et al. 1997).

In experiments to evaluate the relative value of alternate food sources following fires, Mihuc and Minshall (1995) found that unburned coarse particulate material (CPM) and periphyton were important food resources for macroinvertebrate consumers. Burned material, however, was not a significant resource for primary consumers. Trophic generalists (macroinvertebrates capable of using two or more resources for growth) were able to switch food resources as availability shifted, and Mihuc and Minshall (1995) suggested that this adaptability may be especially important to survival in postdisturbance environments.

In some studies, effects of fire on stream benthic communities have been minimal or so brief that they were undetectable (Lotspeich et al. 1970; Ste-
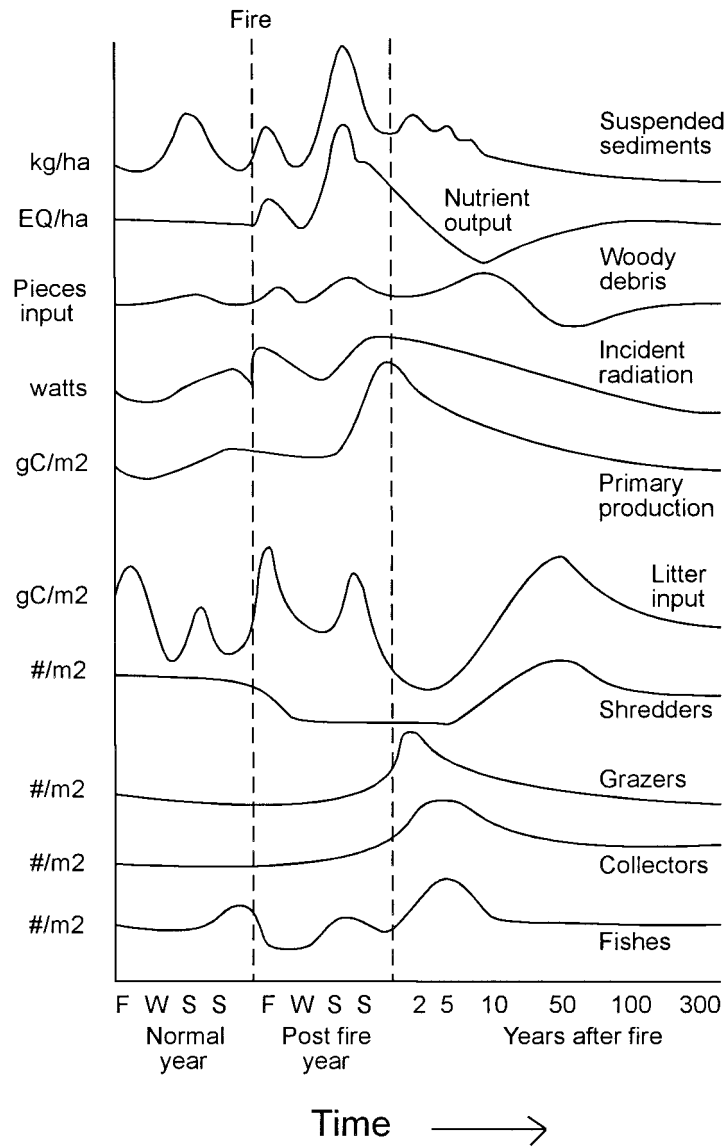
FIGURE 3.—Hypothetical changes in physical, chemical, and biological characteristics of fluvial systems following fire. The letters F, W, S, and S, indicate fall, winter, spring and summer, respectively. (Adapted from G. W. Minshall et al. 1989.)

fan 1977). Following the 1988 fires in Yellowstone National Park, macroinvertebrate abundance fluctuated in four of the larger streams (fifth- and sixth-order); however, species richness and diversity did not decline (Jones et al. 1993). The most ecologically significant change in the these large streams was an apparent shift in functional feeding groups from shredder- and collector-dominated communities (usually associated with allochthonous production in the riparian zone) to scraper- and filter-

feeder-dominated communities (Jones et al. 1993). Scrapers and filter feeders are associated with autochthonous systems (Vannote et al. 1980), and the observed changes were attributed to lowered allochthonous input and greater autochthonous production following the fires.

There is some evidence that changes in stream macroinvertebrate communities can persist for many years. Nine years after 95% of an 825-ha watershed burned in the western Sierra Nevada of

California, Roby (1989) found that macroinvertebrate diversity was lower than estimates from nearby reference streams. Macroinvertebrate density was highest in the burned watershed; however, Chironomidae (a group adapted to disturbed areas dominated by fine sediments; Mihuc et al. 1996), were the most abundant organisms in those areas. Macroinvertebrate diversities were also lower (compared with unburned watersheds) in four other watersheds that had burned from 7 to 23 years prior to the study (Roby 1989). These differences in macroinvertebrates were evident despite the fact that channel profiles in the burned watersheds were similar to prefire conditions.

Minshall et al. (1989) hypothesized that successional development of riparian and terrestrial vegetation would reduce water yield and erosion, allowing macroinvertebrate and periphyton production to increase above prefire levels (Figure 3). In the absence of disturbance, however, increased shading associated with conifer growth eventually reduces riparian production and allochthonous inputs (Minshall et al. 1989). In Yellowstone National Park, Albin (1979) compared a stream in a watershed that had been burned twice (45 and 36 years prior to his study) with a stream from the adjacent watershed that had not burned. Water temperature, water yield, transport of dissolved solids, and seasonal variations in discharge were greater in the stream in the burned watershed. No differences were noted in periphyton accumulation on artificial substrates; however, the stream in the burned watershed had a higher abundance of benthic macroinvertebrates.

Recently, Mihuc et al. (1996) argued that ecological studies of macroinvertebrates in streams should be conducted at the population level because community-level descriptions often disregard trends of individual species. Comparisons of six sites in burned watersheds and four sites in unburned reference watersheds suggested that changes in physical habitat and the availability of food resources were the primary factors affecting postfire response of individual populations. Taxa best adapted to postfire conditions displayed a broad range of preferences for physical habitat, but taxa that required stable riffles or slower stream velocities were less abundant in postfire years.

Fluvial systems: fishes.—Fire-related hydrologic events may result in localized fish deaths (Table 1). At Beaver Creek, Montana (Missouri River basin), an intense rainstorm occurred just 1 d after wildfire burned 26% of the lower drainage, and the associated stream discharge exceeded that of a 100-year flood event (Novak and White 1990). Estimates revealed a drastic decrease in abundance (>99%) and biomass (>98%) of brown trout *Salmo trutta* and rainbow trout (Novak and White 1990). Bozek and Young (1994) reported the death of brook trout *Salvelinus fontinalis,* Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri,* rainbow trout, and Yellowstone cutthroat trout × rainbow trout hybrids following an intense rainstorm 2 years after fire burned most of the watershed (Jones Creek, North Fork Shoshone River, Wyoming). Rinne (1996) reported that two populations of brook trout and one population of rainbow trout in central Arizona and one of the few remaining populations of the endangered Gila trout *O. gilae* in southern New Mexico (Propst et al. 1992) were essentially extirpated following postfire flood events in 1989 and 1990. Similarly, several reaches of two tributaries to the Boise River (southwestern Idaho) appeared to be completely ''defaunated'' following fires in 1992 (Rieman et al. 1997a).

Ultimately, recolonization of fishes into areas where they have been extirpated is influenced by proximity and relative location of refugia, unimpeded routes of access, and the occurrence of complex life history patterns and overlapping generations (Warren and Liss 1980; Rieman and Clayton 1997; Rieman et al. 1997a). Recolonization by fishes is generally rapid if access is adequate. Rieman et al. (1997a) reported that fish were present in defaunated reaches of the Boise River in 1 year and approached densities of unaffected reaches in 1–3 years following fire. Novak and White (1990) noted that rainbow trout density and biomass exceeded prefire estimates in the year following a fire and subsequent flood event. Apparently, spring-spawning adfluvial rainbow trout from the Missouri River contributed to the substantial increases in Beaver Creek. Recolonization of brown trout was not observed, however, perhaps because beaver dams and low discharge limited access to fall-spawning adfluvial brown trout (Novak and White 1990). In some watersheds, abundance of native fish populations has declined, and they have become increasingly isolated in headwater streams because of land-use practices (e.g., logging, grazing, and water diversion) and nonnative fish introductions. In such cases, reduced habitat connectivity has increased the vulnerability of fish populations to disturbance and limited potential recolonization (Medina and Martin 1988; Propst et al. 1992; Rinne 1996). For example, fire has resulted in the extirpation of several isolated fish

populations in streams of the American Southwest (Rinne 1996).

In larger streams, effects of fire on fish populations may be less severe (Lotspeich et al. 1970). In Cache Creek, a fourth-order tributary to the Lamar River in Yellowstone National Park, Gould (1990) found that population abundance of Yellowstone cutthroat trout declined the year following the fires of 1988; however, differences were within the normal range of variation for streams of similar size in the area. After monitoring hydrological regime, stream habitat, water chemistry, and fish populations in fifth- and sixth-order streams for 5 years following these fires, Jones et al. (1993) could not find evidence of negative effects on fish.

Lacustrine systems.—The influence of fire on biological communities of lacustrine environments has not been studied extensively. Despite increased nutrient loading in tributary streams following wildfire in northern Minnesota, neither nutrient concentrations nor phytoplankton abundance in the lakes appeared to change (Wright 1976; Bradbury 1986; Tarapchak and Wright 1986). Although approximately 28% of the Yellowstone Lake watershed burned in 1988, Gresswell (unpublished data) did not find a significant change in annual growth increments of Yellowstone cutthroat trout that could be attributed to increased zooplankton productivity following the fires.

Discussion

Factors Influencing the Effects of Fire in Aquatic Systems

Because initial conditions are critical in determining the outcome of disturbance in complex systems, fire-mediated changes in aquatic systems are contingent on the attributes of the system and fire characteristics, including intensity, severity, and size. Over the long term, physical, chemical, and biological elements of a watershed interact with climate conditions to influence the fire regime, and in the short term, postfire vegetation mosaic interacts with local weather to govern the trajectory and magnitude of change following a fire event. Disentangling the influence of long- and short-term variables is often not possible; however, individual components such as soil, vegetation, geology, topography, geomorphology, and climate may be examined within the context of the more complex whole (Figure 1).

Burn severity and pattern are directly linked to aquatic systems by postfire changes in soil chemistry and soil erosion. Nutrient chemistry is affected by the postfire character of remaining organic soil layers, soil organisms, and vegetation. Physical properties of soil that control water retention are altered by heating, and in some cases, soils become water repellent after severe burns. The amount of vegetation remaining in the watershed directly influences runoff and erosion by physically mediating the force of precipitation on soil surfaces, altering the evapotranspiration cycle, and providing soil stability through root systems. Runoff rate and pattern and subsequent erosion potential are directly affected by the amount of organic debris left on the watershed. Burn characteristics also modify patterns of revegetation because the amount and type of new vegetation are related to seed availability, opportunities for resprouting, and changes in water yield and nutrient retention in the watershed.

Geology is an important variable in the hydrological cycle of individual watersheds. Lithological influence on soil and water chemistry is substantial; therefore, under postfire conditions, soil type contributes directly to nutrient loading of subsequent runoff. Nutrient availability for vegetation development also varies with soil type. Water repellency of soils is related to soil texture, fire intensity, and vegetation type. Although hydrophobicity can often occur in the absence of fire, coarse-textured soils appear to be especially susceptible to this condition during fires because of their low heat capacity, high porosity, and the small surface area that is vulnerable to coating with organic compounds produced by burning.

Soil distribution, microclimate, and other factors that determine the distribution of vegetation across the landscape are ultimately controlled by landform and geological processes that form them. Alterations of vegetation, soils, and hydrology are short-term geomorphic responses to a single fire; however, on a longer time scale, topography often modifies fire behavior and the effects of fire on aquatic systems. In watersheds that are prone to erosion, the primary effect of a single fire may be a short-term alteration of hydrological and erosional processes. Because the proportion of a watershed that is burned influences the magnitude and extent of the postfire changes, smaller drainages in headwater areas often exhibit the greatest fire-related alterations.

Modification of channel morphology and increased sedimentation may substantially influence components of biological systems, both negatively and positively. In highly erosive landscapes, fre-

quent fire may influence sedimentation, but across broad geographical areas, fire is subordinate to other factors (e.g., anthropogenic land-use activities) that contribute to sedimentation and stream channel modification. Although increased sediment loads may ultimately lead to increased production and eutrophication in lakes (Bradbury 1986; Spencer 1991), research thus far does not indicate significant changes in nutrient enrichment, plankton production, or fish growth in lacustrine systems as a result of fire.

Periodic variations in the influx of sediment and coarse woody debris contribute to aquatic habitat heterogeneity reflected in diverse fish communities. Woody debris is critical for stream habitat heterogeneity and stability for fishes, and in some cases, fires result in a substantial increase in the amount of woody debris entering the system. The scale of postfire effects on the accumulation of woody debris depends on the prefire vegetation and the severity of the fire. In extreme cases where fire consumes a large proportion of the vegetation (including instream debris jams) or water yield is substantially increased, woody debris loading may decline until vegetational development is sufficient to provide new sources of wood.

Vegetation also influences the severity and pattern of fires, and at least two systems for describing fire regimes are based on dominant or potential vegetation (Agee 1993; Morgan et al. 1995). Vegetation integrates physical components of the terrestrial ecosystem with weather over the short-term, and climate at a greater temporal scale. The reduction or removal of the overhead canopy in riparian areas is frequently associated with a decrease in stream shading and a concomitant increase in water temperature. Temperature changes are generally not lethal to aquatic organisms, however, and water temperatures decline as vegetation becomes reestablished.

Climate exerts substantial control on fire and its effect on aquatic ecosystems. Ultimately, the physical, chemical, and biological components of the terrestrial portions of an aquatic system interact with climatological controls (both pre- and postfire) to modify the aquatic environment (Figure 1). Depending on the specific outcome of this interaction, the biological community may experience change on several levels.

Effects on Native Species

In many cases, the effects of fire on the biotic community in aquatic systems are subtle. Terrestrial habitat patches directly influence aquatic habitats (White and Pickett 1985; Frissell et al. 1986), and it is increasingly apparent that fire plays an important role in maintaining heterogeneity in both terrestrial and aquatic systems. Perturbations associated with hydrologic processes affect postfire persistence of fishes, benthic macroinvertebrates, and diatoms in fluvial systems, and there is some evidence of mortality directly associated with the fire event. In extreme cases, fish populations may be extirpated from some stream reaches or segments, but where streams are sufficiently connected with appropriate species refugia, fish recolonization is generally rapid. In fact, species persistence in aquatic systems is probably linked to adaptation to periodic perturbations, such as those resulting from fire (Hanski 1991; Rieman and McIntyre 1995; Schlosser and Angermeier 1995).

In individual watersheds, the influence of fire events appears to be greatest at spatial scales of 10^2–10^3 m and temporal scales of 10^1–10^2 years; for second- or third-order streams these scales relate to stream segments, geomorphic reaches, individual habitat units, and microhabitats (Frissell et al. 1986). Repeated fires within a watershed over periods of 10^3 years may influence larger areas, and even entire second- or third-order stream systems (10^3–10^4 m) because repeated fires can alter the vegetation community; soil conditions; and frequency, occurrence, and distribution of floods, debris flows, and landslides that control channel and floodplain geomorphology (Poff and Ward 1990). At greater spatial scales ($>10^3$ m), however, watershed components (i.e., general valley configuration, juxtaposition of stream segment types, and stream gradient) are probably not affected greatly by fire (Figure 4).

Paleoecologists have suggested that species lineages persist on the order of 10^6–10^8 years (Bennett 1990), and to survive as a species implies the ability to adapt to a range of environmental variations occurring on different temporal and spatial scales (Barnosky 1987; Bartlein and Prentice 1989). Bennett (1990) proposed a four-tiered hierarchy of time scales that describe the range of these variations including ecological time (10^3 years), cycles of earth orbital eccentricity (Milankovitch cycles; 10^4–10^5 years), geological time (10^6 years), and mass extinctions (26×10^6 years). For example, salmonids have evolved in North America since the late Miocene (approximately 6×10^6 years; Stearley and Smith 1993), and, there is little doubt that their evolution included the development of strategies to survive perturbations
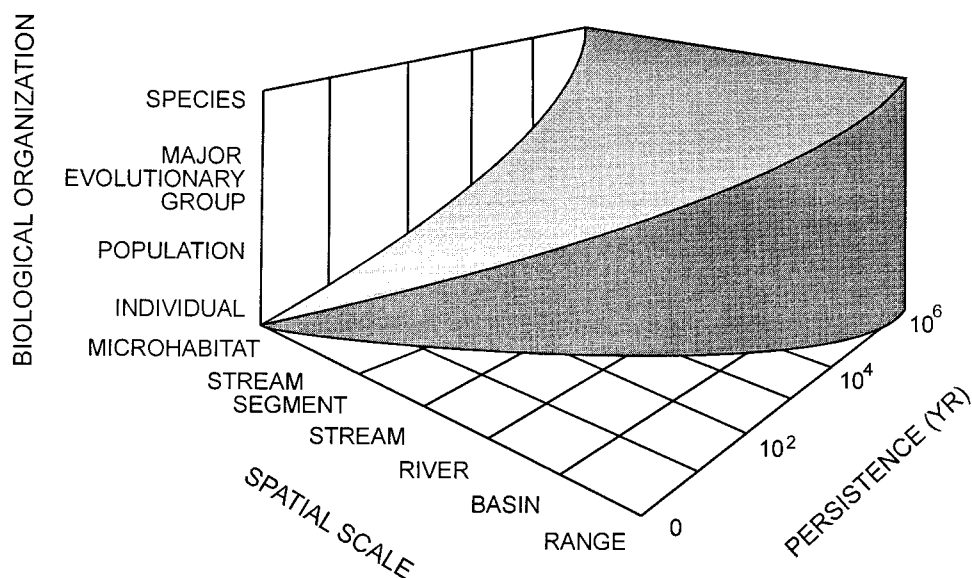
FIGURE 4.—Hierarchical model showing biological levels of organization for stream salmonids and how they vary on different spatial and temporal scales (adapted from Currens 1997).

occurring at the frequency of Holocene wildland fires (10^0–10^2 years).

In contrast, local fish populations are relatively ephemeral, especially in highly heterogeneous and frequently fluctuating environments (Larson et al. 1995; Rieman and McIntyre 1995; Schlosser and Angermeier 1995). Ultimately, persistence of a biological system (e.g., life history type, population, metapopulation, subspecies, species, and community) is dependent on the interplay of environmental and biological components, and life history diversity is a means of spreading risk of extirpation in dynamic environments (sensu den Boer 1968). Effects of perturbation at various levels in the stream–system hierarchy, however, influence organisms differentially. Effects of physical or chemical alteration of a habitat patch are greatest on those individuals and local populations that are least mobile, and reinvasion is most rapid by organisms with high mobility. Stream reach, and possibly stream segments, are most affected by fire events, and therefore, responses may extend to the macroinvertebrate community level and last for decades (Molles 1982; Wallace 1990). Effects of fire on fluvial fishes are probably greatest at the population or individual level (Figure 4). In most aquatic ecosystems, fire is a natural process that has been occurring for thousands of years or more, and in systems with adequate connectivity and sufficient species pool, there is no evidence that fire-

mediated perturbations would result in reduced persistence in most groups of organisms.

Relationship to Anthropogenic Disturbance

The effects of fire are related to, and are modified by, anthropogenic disturbance. For example, during the past century fire suppression has altered the fire regime in some vegetation types (especially those areas with naturally high fire frequency, i.e., <5/century); subsequently, the probability of large stand-replacing fires has increased (Kilgore 1973; Agee 1993; Huff et al. 1995). Where fire suppression has been especially effective, stand structure has become more uniform, and fine fuels have accumulated (Heinselman 1973; Kilgore 1981; Agee 1993). Fire suppression, clear-cut logging, and livestock grazing have interacted to encourage increased landscape homogeneity. Regional diversity of plants and animals associated with habitat complexity may be substantially altered (Agee 1993).

Although fire suppression may have increased the probability of stand-replacing fire in some forest types, influence of climate change and local climate anomalies must also be considered. For instance, paleoecological data suggest that intervals between fires are not static; fire frequency and predictability vary continuously through time in response to climate change (Cwynar 1987; Johnson and Larsen 1991; Swetnam 1993; Millspaugh

and Whitlock 1995; Long et al. 1998). Fire is strongly affected by landscape-scale features such as topography and vegetation pattern, but these parameters are most important when burning conditions, such as wind and fuel moisture, are not excessive. In Yellowstone National Park, the fires of 1988 appeared to have been influenced more by drought conditions and strong winds during the summer than by accumulated fuels; virtually all forest age and fuel categories burned (Christensen et al. 1989). Fire suppression had little effect during this event. Interestingly, Brown et al. (1994) found that when compared with a recent period (1979–1990), stand-replacement fires were 1.9 times greater in the presettlement period (pre-1935). Additionally, Turner and Romme (1994) have suggested that climate is the primary factor in the behavior and spread of crown fires.

Because fire and anthropogenic management activities are not mutually exclusive, their interaction may cause more substantial change in aquatic systems than either would alone. Negative effects of logging are also associated with fire suppression and postfire salvage logging. Erosion from construction of fire lines and roads may be the most significant negative effect, but soil exposure and compaction effects of machine or tractor piling operations substantially increase erosion. Removal of woody debris increases the probability of erosion and eliminates an important structural component that leads to recovery of terrestrial and aquatic systems. Postfire seeding of annual grasses may actually increase runoff and retard natural vegetation. In the broadest sense, salvage logging can increase habitat homogeneity of the postfire landscape and, thereby, significantly alters postfire ecological processes.

In addition, there is substantial evidence that anthropogenic activities have led directly to broad-scale aquatic habitat destruction and the extirpation and extinction of aquatic taxa (Nehlsen et al. 1991; Rieman et al. 1997b; Thurow et al. 1997). Near extinction of beaver *Castor canadensis* on a continental scale over the last two centuries caused unidirectional changes in stream hydrology and ecology (Naiman et al. 1988). Timber harvest and grazing have also had spatially extensive effects on aquatic ecosystems in North America (Frissell 1993; McIntosh et al. 1994; Wissmar et al. 1994). Whereas fire is an integral part of terrestrial and aquatic ecosystems that promotes landscape and habitat heterogeneity (Pickett and White 1985), anthropogenic reduction and removal of beaver, timber harvest, fire suppression, and livestock

grazing are not. These human disturbances are manifest over broad spatial scales in a short period of time (<150 years), and as a result, they have promoted homogeneity of terrestrial and aquatic ecosystems at all spatial scales (Ebersole et al. 1997).

It is apparent, however, that in areas where population isolation is low and life history organization is complex, aquatic organisms are adapted to even the most destructive effects of fire. Current evidence suggests that even in the case of extensive, high-severity fires, local extirpation of fishes is patchy, and recolonization is rapid. Long-term detrimental effects on fish populations have been limited to areas where native populations have declined and become increasingly isolated as a result of anthropogenic activities. These observations strongly support a strategy of protecting aquatic communities in areas where they have remained robust and restoring habitat structure and life history complexity where possible. Because it is unlikely that humans will be able to fireproof forested ecosystems, perhaps the most effective means of ameliorating the negative consequences of fires on aquatic systems is to protect the evolutionary capacity of these systems to respond to disturbance.

Implication for Future Research

There are three general implications for future research resulting from this review. First, the effects of fire can rarely be isolated from anthropogenic activities. Evaluations have frequently been conducted on study sites that were also influenced by logging (preburn or postburn), reseeding, chemical fire retardants, fire lines and other soil disturbance during fire suppression, road construction, or other management actions that confound interpretation of causal connections. Although it may not be possible to control for anthropogenic influences, it is important to recognize their potential influence on study results, and these factors should be addressed explicitly in research design. Furthermore, these factors should be detailed in published accounts so that potential confounding factors can be identified. This is especially critical in cases where there is evidence that current vegetation and fire behavior have been altered by past fire suppression activities.

Second, the spatial scale of studies assessing effects of fire has generally been restricted to point observations and stream transects, and attempts to generalize effects to aquatic habitats at the landscape or regional scale have been rare. Even recent studies that purport to view the effects of fire on

a landscape scale have not been statistically or conceptually designed to expand interpretation of results beyond the sample site. Studies based on representative stream reaches have substantial shortcomings, and it is important to use more statistically robust methods for expanding results to larger spatial scales (e.g., Hankin and Reeves 1988; Overton et al. 1993). Recent improvements in Geographical Information Systems provide additional tools that are essential to broadening the scale of future fire effects research and providing needed geographic context for the interpretation of results.

Finally, the temporal scale of aquatic ecosystem response to fire has been largely ignored. Although vegetation reconstruction from dendrochronological and paleoecological records provides an extended view of successional trajectories and dominant vegetation types, studies that follow long-term system response of aquatic systems to fire are rare. There are a growing number of studies that have extended postfire monitoring beyond 5 years, but to truly understand the effects of fire across a broad geographic area, it will be necessary to expand the temporal extent of future studies. The restricted temporal scale of postfire research may be especially important in cases where fires are extensive and the effects are not uniform, either spatially or temporally, across the landscape.

Acknowledgments

References

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Ahlgren, I. F., and C. E. Ahlgren. 1960. Ecological effects of forest fires. Botanical Review 26:483–533.

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

Amaranthus, M., H. Jubas, and D. Arthur. 1989. Stream shading, summer streamflow, and maximum water temperature following intense wildfire in headwater streams. U.S. Forest Service General Technical Report PSW-109:75–78.

Anderson, H. W. 1976. Fire effects on water supply, floods, and sedimentation. Proceedings, Tall Timbers Fire Ecology Conference 15:249–260.

Balling, R. C., Jr., G. A. Meyer, and S. G. Wells. 1992. Climate change in Yellowstone National Park: is the drought-related risk of wildfires increasing? Climatic Change 22:35–45.

Barnosky, C. W. 1987. Response of vegetation to climatic changes of different duration in the late Neogene. Trends in Ecology and Evolution 2:247–250.

Bartlein, P. J., and I. C. Prentice. 1989. Orbital variations, climate and paleoecology. Trends in Ecology and Evolution 4:195–199.

Bayley, S. E., D. W. Schindler, K. G. Beaty, B. R. Parker, and M. P. Stainton. 1992. Effects of multiple fires on nutrient yields from streams draining boreal forest and fen watersheds: nitrogen and phosphorus. Canadian Journal of Fisheries and Aquatic Sciences 49:584–596.

Beaty, K. G. 1994. Sediment transport in a small stream following two successive forest fires. Canadian Journal of Fisheries and Aquatic Sciences 51:2723–2733.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Bennett, K. D. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. Paleobiology 16:11–21.

Beschta, R. L. 1990. Effects of fire on water quantity and quality. Pages 219–232 in J. D. Walstad, S. R. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.

Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191–232 in E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington, Institute of Forestry Resources, Contribution 57, Seattle.

Bozek, M. A., and M. K. Young. 1994. Fish mortality resulting from delayed effects of fire in the Greater Yellowstone Ecosystem. Great Basin Naturalist 54: 91–95.

Bradbury, J. P. 1986. Effects of forest fire and other disturbances on wilderness lakes in northeastern Minnesota II, paleolimnology. Archiv für Hydrobiologie 106:203–217.

Brass, J. A., V. G. Ambrosia, P. J. Riggan, and P. D. Sebesta. 1996. Consequences of fire on aquatic nitrate and phosphate dynamics in Yellowstone Na-

tional Park. Pages 53–57 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the Greater Yellowstone Ecosystem: the ecological implications of fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, Washington.

Brown, G. W., A. R. Gahler, and R. B. Marston. 1973. Nutrient losses after clear-cut logging and slash burning in the Oregon Coast Range. Water Resources Research 9:1450–1453.

Brown, G. W., and J. T. Krygier. 1971. Clear-cut logging and sediment production in the Oregon Coast Range. Water Resources Research 7:1189–1198.

Brown, J. K. 1990. Effects of fire on streams. Pages 106–110 *in* F. Richardson and R. H. Hamre, editors. Wild trout IV: proceedings of the symposium. Trout Unlimited, Arlington, Virginia.

Brown, J. K., S. F. Arno, S. W. Barrett, and J. P. Menakis. 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway–Bitterroot Wilderness. International Journal of Wildland Fire 4:157–168.

Christensen, N. L., and twelve coauthors. 1989. Interpreting the Yellowstone fires of 1988. BioScience 89:678–685.

Clayton, J. L. 1976. Nutrient gains to adjacent ecosystems during a forest fire: an evaluation. Forest Science 22:162–166.

Covington, W. W., and five coauthors. 1994. Historical and anticipated changes in forest ecosystems of the inland West of the United States. Journal of Sustainable Forestry 2:13–63.

Cummins, K. W. 1978. Ecology and distribution of aquatic insects. Pages 29–31 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Currens, K. R. 1997. Evolution and risk in conservation of Pacific salmon. Doctoral dissertation. Oregon State University, Corvallis.

Cushing, C. E., Jr., and P. A. Olson. 1963. Effects of weed burning on stream conditions. Transactions of the American Fisheries Society 92:303–305.

Cwynar, L. C. 1987. Fire and the forest history of the North Cascade Range. Ecology 68:791–802.

DeBano, L. F., P. H. Dunn, and C. E. Conrad. 1977. Fire's effects on physical and chemical properties of chaparral soils. U.S. Forest Service General Technical Report WO-3:65–74.

DeByle, N. V., and P. E. Packer. 1972. Plant nutrients and soil losses in overland flow from burned forest clearcuts. Pages 296–305 *in* S. C. Crallany, T. G. McLaughlin, and W. D. Striffler, editors. Watersheds in transition. American Water Resources Association, Urbana, Illinois.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165–194.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 1997. Restoration of stream habitats in managed landscapes in the western USA: restoration as re-expression of habitat capacity. Environmental Management 21:1–14.

Everest, F. H., and five coauthors. 1987. Fine sediment and salmonid production: a paradox. Pages 98–142 *in* E. O. Salo and T. W. Cundy, editors. Stream side management: forestry and fishery interactions. University of Washington, Institute of Forest Research, Contribution 57, Seattle.

Feller, M. C. 1981. Effects of clearcutting and slash-burning on stream temperature in southwestern British Columbia. Water Resources Bulletin 17:863–867.

Fredriksen, R. L. 1971. Comparative chemical water quality—natural and disturbed streams following logging and slash burning. Pages 125–137 *in* J. T. Krygier and J. D. Hall, editors. Forest land uses and stream environment. Oregon State University, Continuing Education Publications, Corvallis.

Frissell, C. A. 1993. Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). Conservation Biology 7:342–354.

Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. 1997. A resource in crisis: changing the measure of salmon management. Pages 411–444 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.

Gould, W. R. 1990. The cutthroat trout populations of Cache Creek, Yellowstone National Park, during the autumns of 1988 and 1989. Report to the Yellowstone Fishery Assistance Office, Montana Cooperative Fishery Research Unit, Montana State University, Bozeman.

Gray, J. R. A., and J. M. Edington. 1969. Effect of woodland clearance on stream temperature. Journal of the Fisheries Research Board of Canada 26:399–403.

Grier, C. C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Canadian Journal of Forest Research 5:599–607.

Gruell, G. E. 1985. Fire on the early western landscape: an annotated record of wildland fires 1776–1900. Northwest Science 59:97–107.

Hakala, J. B., R. K. Seemel, R. Richey, and J. E. Keurtz. 1971. Fire effects and rehabilitation methods: Swanson–Russian River fires. Pages 87–89 *in* C. W. Slaughter, R. J. Barry, and G. M. Hansen, editors. Fire in the northern environment. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Hall, J. D., and R. L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. Pages 335–375 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.

Hankin, D. G., and G. H. Reeves. 1988. Estimating total

fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45:834–844.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17–38.

Harmon, M. E., and nine coauthors. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quaternary Research 3:329–382.

Helvey, J. D. 1972. First-year effects of wildfire on water yield and stream temperature in north-central Washington. Pages 308–312 in S. C. Callany, T. G. McLaughlin, and W. D. Striffler, editors. Watersheds in transition. American Water Resources Association, Proceedings Series 14, Urbana, Illinois.

Helvey, J. D. 1980. Effects of a north-central Washington wildfire on runoff and sediment production. Water Resources Bulletin 16:627–634.

Helvey, J. D., A. R. Tiedemann, and W. B. Fowler. 1976. Some climatic and hydrologic effects of wildfire in Washington state. Proceedings, Tall Timbers Fire Ecology Conference 15:201–221.

Huff, M. H., and six coauthors. 1995. Historical and current forest landscapes in eastern Oregon and Washington. Part II. Linking vegetation characteristics to potential fire behavior and related smoke production. U.S. Forest Service General Technical Report PNW-GTR-355.

Hunter, M. L., Jr. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65:115–120.

Johnson, C. M., and P. R. Needham. 1966. Ionic composition of Sagehen Creek, California, following an adjacent fire. Ecology 47:636–639.

Johnson, E. A., and C. P. S. Larsen. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. Ecology 72:194–201.

Jones, R. D., and five coauthors. 1993. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1992, Yellowstone National Park, Wyoming.

Jones, R. D., and six coauthors. 1989. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1988, Yellowstone National Park, Wyoming.

Jones, R. D., J. D. Varley, D. E. Jennings, S. M. Rubrecht, and R. E. Gresswell. 1979. Fishery and aquatic management program in Yellowstone National Park. U.S. Fish and Wildlife Service, Technical Report for 1978, Yellowstone National Park, Wyoming.

Kilgore, B. M. 1973. The ecological role of fire in Sierran conifer forests. Quaternary Research 3:496–513.

Kilgore, B. M. 1981. Fire in ecosystem distribution and structure: western forests and scrublands. U.S. Forest Service General Technical Report WO-26:58–89.

Kilham, S. S., E. C. Theriot, and S. C. Fritz. 1996. Linking planktonic diatoms and climate change using resource theory in the large lakes of the Yellowstone ecosystem. Limnology and Oceanography 41:1052–1062.

Klock, G. O., and J. D. Helvey. 1976. Soil-water trends following wildfire on the Entiat Experimental Forest. Proceedings, Tall Timbers Fire Ecology Conference 15:193–200.

Knight, D. H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. Pages 59–83 in M. G. Turner, editor. Landscape heterogeneity and disturbance. Springer-Verlag, New York.

Kozlowski, T. T., and C. E. Ahlgren, editors. 1974. Fire and ecosystems. Academic Press, New York.

La Point, T. W., M. Parker, C. A. Brewer, and M. Crossey. 1983. Impact of fire on recreation stream water quality and spawning habitat. Final report (Cooperative Agreement 28-C2–222) of University of Wyoming, Department of Zoology and Physiology to U.S. Forest Service, Laramie, Wyoming.

Larson, G. L., S. E. Moore, and B. Carter. 1995. Ebb and flow of encroachment by nonnative rainbow trout in a small stream in the southern Appalachian mountains. Transaction of the American Fisheries Society 124:613–622.

Lathrop, R. G., Jr. 1994. Impacts of the 1988 wildfires on the water quality of Yellowstone and Lewis lakes, Wyoming. International Journal of Wildland Fire 4:169–175.

Lathrop, R. G., Jr., J. D. Vande Castle, and J. A. Brass. 1994. Monitoring changes in Greater Yellowstone Lake water quality following the 1988 wildfires. Geocarto International 3:49–57.

Lawrence, D. E., and G. W. Minshall. 1994. Short- and long-term changes in riparian zone vegetation and stream macroinvertebrate community structure. Pages 171–184 in D. G. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem. U.S. National Park Service, Natural Resources Publication Office, Technical Report NPS/NRYELL/NRTR-93/XX, Denver.

Long, C. J., C. Whitlock, P. J. Bartlein, and S. H. Millspaugh. 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. Canadian Journal of Forest Research. 28:774–787.

Lotspeich, F. B., E. W. Mueller, and P. J. Frey. 1970. Effects of large scale forest fires on water quality in interior Alaska. Federal Water Pollution Control Administration, Alaska Water Laboratory, College, Alaska.

Marston, R. A., and D. H. Haire. 1990. Runoff and soil loss following the 1988 Yellowstone fires. Great Plains–Rocky Mountain Geographical Journal 18:1–8.

McColl, J. G., and D. F. Grigal. 1975. Forest fire: effects on phosphorus movement to lakes. Science 188:1109–1111.

McColl, J. G., and D. F. Grigal. 1977. Nutrient changes following a forest wildfire in Minnesota: effects in watersheds with differing soils. Oikos 28:105–112.

McIntosh, B. A., and six coauthors. 1994. Historical changes in fish habitat for select river basins in eastern Oregon and Washington. Northwest Science 68:36–53.

McIntyre, M. J., and G. W. Minshall. 1996. Changes in transport and retention of coarse particulate organic matter in streams subjected to fire. Pages 59–75 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the Greater Yellowstone Ecosystem: the ecological implications of fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, Washington.

McMahon, T. E., and D. S. deCalesta. 1990. Effects of fire on fish and wildlife. Pages 233–250 *in* J. D. Walstad, S. R. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.

McNabb, D. H., F. Gaweda, and H. A. Froehlich. 1989. Infiltration, water repellency, and soil moisture content after broadcast burning a forest site in southwest Oregon. Journal of Soil and Water Conservation 44:87–90.

McNabb, D. H., and F. J. Swanson. 1990. Effects of fire on soil erosion. Pages 159–176 *in* J. D. Walstad, S. R. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis.

Medina, A. L., and C. Martin. 1988. Stream channel and vegetation changes in sections of McKnight Creek, New Mexico. Great Basin Naturalist 48:378–381.

Meyer, G. A. 1993. Holocene and modern geomorphic response to forest fires and climate change in Yellowstone National Park. Doctoral dissertation. University of New Mexico, Albuquerque.

Meyer, G. A., S. G. Wells, R. C. Balling, Jr., and A. J. T. Jull. 1992. Response of alluvial systems to fire and climate change in Yellowstone National Park. Nature (London) 357:147–150.

Meyer, G. A., S. G. Wells, and A. J. T. Jull. 1995. Fire and alluvial chronology in Yellowstone National Park: climatic and intrinsic controls on Holocene geomorphic processes. Geological Society of America Bulletin 107:1211–1230.

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.

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

Millspaugh, S. H., and C. Whitlock. 1995. A 750-year fire history based on lake sediment records in central Yellowstone National Park. Holocene 5:283–292.

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 174–177 *in* F. Richardson and R. H. Hamre, editors. Wild trout IV: proceedings of the symposium. Trout Unlimited, Arlington, Virginia

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.

Minshall, G. W., J. T. Brock, and J. D. Varley. 1989. Wildfires 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, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 54:2509–2525.

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

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

Mooney, H. A., T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. 1981. Fire regimes and ecosystem properties. U.S. Forest Service General Technical Report WO-26.

Morgan, P., S. C. Bunting, A. E. Black, T. Merrill, and S. Barrett. 1995. Fire regimes in the interior Columbia River basin: past and present. U.S. Forest Service, Intermountain Fire Sciences Laboratory, Intermountain Research Station, Final Report, RJVA-INT-94913, Missoula, Montana.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration on North American streams by beaver. BioScience 38:753–762.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nobel, E. L., and L. J. Lundeen. 1971. Analysis of rehabilitation treatment alternatives for sediment control. Pages 86–96 *in* J. T. Krygier and J. D. Hall, editors. Forest land uses and stream environment. Oregon State University, Continuing Education Publications, Corvallis.

Norris, L. A., and W. L. Webb. 1989. Effects of fire retardant on water quality. U.S. Forest Service General Technical Report PSW-109:79–86.

Novak, M. A., and R. G. White. 1990. Impact of fire and flood on the trout population of Beaver Creek, upper Missouri basin, Montana. Pages 120–127 *in* F. Richardson and R. H. Hamre, editors. Wild trout IV: proceedings of the symposium. Trout Unlimited, Arlington, Virginia.

Overton, J. McC., T. C. Young, and W. S. Overton. 1993. Using 'found' data to augment a probability sample: procedure and case study. Environmental Monitoring and Assessment 26:65–83.

Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. Pages 371–384 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management 14:629–645.

Price, C., and D. Rind. 1994. The impact of a $2\times CO_2$ climate on lightning-caused fires. Journal of Climate 7:1484–1494.

Propst, D. L., J. A. Stefferud, and P. R. Turner. 1992. Conservation and status of Gila trout, Oncorhynchus gilae. Southwestern Naturalist 37:117–125.

Pyne, S. J. 1984. Introduction to wildland fire: fire management in the United States. Wiley, New York.

Quigley, T. M., R. W. Haynes, and R. T. Graham, editors. 1996. Integrated scientific assessment for ecosystem management in the interior Columbia basin and portions of the Klamath and Great basins. U.S. Forest Service General Technical Report PNW-GTR-382.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334–349 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Reeves, G. H., F. H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. Transactions of the American Fisheries Society 122:309–317.

Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environmental Management 14:647–659.

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

Rieman, B. E., and J. L. Clayton. 1997. Fire and fish: issues of forest health and conservation of native fishes. Fisheries 22(11):6–15.

Rieman, B. E., D. Lee, G. Chandler, and D. Myers. 1997a. Does wildfire threaten extinction for salmonids: responses of redband trout and bull trout following recent large fires on the Boise National Forest. Pages 47–57 in J. Greenlee, editor. Proceedings of the symposium on fire effects on threatened and endangered species and habitats. International Association of Wildland Fire, Fairfield, Washington.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997b. Distribution, status, and likely future trends of bull trout in the interior Columbia River basin and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

Rieman, B. E., and J. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transaction of the American Fisheries Society 124:285–296.

Rinne, J. N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. North American Journal of Fisheries Management 16:653–658.

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

Robinson, C. T., G. W. Minshall, and S. R. Rushforth. 1994a. The effects of the 1988 wildfires on diatom assemblages in streams of Yellowstone National Park. Pages 247–257 in D. G. Despain, editor. Plants and their environments: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem. U.S. National Park Service, Natural Resources Publication Office, Technical Report NPS/NRYELL/NRTR-93/XX, Denver.

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

Roby, K. B. 1989. Watershed response and recovery from the Will fire: ten years of observation. U.S. Forest Service General Technical Report PSW-109: 131–136.

Schindler, D. W., and five coauthors. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Canadian Journal of Fisheries and Aquatic Sciences 37:328–334.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem; defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Schullery, P. 1989. The fires and fire policy. BioScience 39:686–694.

Sedell, J. R., and C. N. Dahm. 1984. Catastrophic disturbances to stream ecosystems: volcanism and clear-cut logging. Pages 531–539 in M. J. Klug and C. A. Reddy, editors. Current perspectives in microbial ecology. American Society for Microbiology, Washington, D.C.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711–724.

Sellers, R. E., and D. G. Despain. 1976. Fire manage-

ment in Yellowstone National Park. Proceedings, Tall Timbers Fire Ecology Conference 14:99–113.

Spencer, C. N. 1991. Evaluation of historical sediment deposition related to land use through analysis of lake sediments. Pages 19–39 *in* Flathead basin forest practices water quality and fisheries cooperative program, final report. Flathead Basin Commission, Kalispell, Montana.

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

Stearley, R. F., and G. R. Smith. 1993. Phylogeny of the Pacific trouts and salmons (*Oncorhynchus*) and genera of the family Salmonidae. Transactions of the American Fisheries Society 122:1–33.

Stefan, D. C. 1977. Effects of a forest fire upon the benthic community of a mountain stream in northeast Idaho. Master's thesis. University of Montana, Missoula.

Stottlemyer, R. 1987. Ecosystem nutrient release from a large fire, Yellowstone National Park. *In* Ninth Conference on Fire and Forest Meteorology, American Meteorological Society, Boston.

Strauss, D., L. Bednar, and R. Mees. 1989. Do one percent of forest fires cause ninety-nine percent of the damage? Forest Science 35:319–328.

Swanson, F. J. 1981. Fire and geomorphic process. U.S. Forest Service General Technical Report WO-26: 401–420.

Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. G. Campbell. 1982. Land–water interactions: the riparian zone. US–IBP Synthesis Series 14:267–291.

Swanson, F. J., J. A. Jones, D. O. Wallin, and J. H. Cissel. 1994. Natural variability—implications for ecosystem management. Pages 80–94 *in* M. E. Jensen and P. S. Bourgeron, editors. Volume II: ecosystem management: principles and applications. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Swanson, F. J., and G. W. Lienkaemper. 1978. Physical consequences of large organic debris in Pacific Northwest streams. U.S. Forest Service General Technical Report PNW-69.

Swanston, D. N. 1971. Principal mass movement processes influenced by logging, road building, and fire. Pages 29–39 *in* J. T. Krygier and J. D. Hall, editors. Forest land uses and stream environment. Oregon State University, Corvallis.

Swanston, D. N. 1991. Natural processes. Pages 139–179 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Swanston, D. N., and F. J. Swanson. 1976. Timber harvesting, mass erosion, and steepland forest geomorphology in the Pacific Northwest. Pages 199–211 *in* D. R. Coates, editor. Geomorphology and engineering. Dowden, Hutchinson, and Ross, Stroudsburg, Pennsylvania.

Swetnam, T. W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885–889.

Tarapchak, S. J., and H. E. Wright, Jr. 1986. Effects of forest fire and other disturbances on wilderness lakes in northeastern Minnesota I. Limnology. Archiv für Hydrobiologie 106:177–202.

Theriot, E. C., S. C. Fritz, and R. E. Gresswell. 1997. Long-term limnological data from the larger lakes of Yellowstone National Park. Arctic and Alpine Research 29:304–314.

Thurow, R. F., D.C. Lee, and B. E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia basin and portions of the Klamath River and Great basins. North American Journal of Fisheries Management 17:1094–1110.

Tiedemann, A. R., and six coauthors. 1979. Effects of fire on water: a state-of-knowledge review. U.S. Forest Service General Technical Report WO-10.

Troendle, C. A., and G. S. Bevenger. 1996. Effect of fire on streamflow and sediment transport Shoshone National Forest, Wyoming. Pages 43–52 *in* J. Greenlee, editor. Proceedings of the second biennial conference on the Greater Yellowstone Ecosystem: the ecological implications of fire in Greater Yellowstone. International Association of Wildland Fire, Fairfield, Washington.

Trotter, E. H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. Journal of the North American Benthological Society 9:141–156.

Trush, W. J. 1990. Salmonid geomorphology. Pages 163–169 *in* F. Richardson and R. H. Hamre, editors. Wild trout IV: proceedings of the symposium. Trout Unlimited, Arlington, Virginia.

Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park. Journal of Vegetation Science 5:731–742.

Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9:59–77.

Uhl, C., and C. F. Jordan. 1984. Succession and nutrient dynamics following cutting and burning in Amazonia. Ecology 65:1476–1490.

Van Meter, W. P., and C. E. Hardy. 1975. Predicting effects on fish of fire retardants in streams. U.S. Forest Service Research Paper INT-166.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Van Sickle, J., and S. V. Gregory. 1990. Modeling inputs of large woody debris to streams from falling trees. Canadian Journal of Forest Research 20:1593–1601.

Wallace, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environmental Management 14:605–620.

Warren, C. E., and W. J. Liss. 1980. Adaptation to aquatic environments. Pages 15–40 *in* R. T. Lackey and L. Nielsen, editors. Fisheries management. Blackwell Scientific Publications, Oxford, UK.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages

3–13 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego.

White, W. D. 1996. Geomorphic response of six headwater basins fifteen years after the La Mesa fire, Bandelier National Monument. U.S. Forest Service General Technical Report RM-GTR-286:95–113.

Wissmar, R. C., and five coauthors. 1994. A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1800s–1990s). Northwest Science 68:1–35.

Woodward, D. F. 1989. The Yellowstone fires: assessing the potential for ash in runoff water to reduce survival and growth of cutthroat trout. Preliminary Report to the U.S. National Park Service, U.S. Fish and Wildlife Service, National Fisheries Contaminant Research Center, Jackson Field Research Station, Jackson, Wyoming.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology. Wiley, New York.

Wright, H. E., Jr. 1974. Landscape development, forest fires, and wilderness management. Science 186:487–495.

Wright, H. E., Jr., and M. L. Heinselman. 1973. Introduction. Quaternary Research 3:319–328.

Wright, R. F. 1976. The impact of forest fire on the nutrient influxes to small lakes in northeastern Minnesota. Ecology 57:649–663.

Young, M. K. 1994. Movement and characteristics of stream-borne coarse woody debris in adjacent burned and undisturbed watersheds in Wyoming. Canadian Journal of Forest Research 24:1933–1938.

Yount, J. D., and G. J. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance—a narrative review of case studies. Environmental Management 14:547–569.