Biodiversity bill update

In its second year before Congress, the biological diversity bill has gained additional cosponsors in both the House and Senate and continues to wind its way through the legislative process. At press time, HR 1268, introduced by James H. Scheuer (D–NY), had advanced beyond its predecessor (*BioScience* 38: 455) by winning the approval of the House Science and Technology Committee and was awaiting hearings before the Merchant Marine and Fisheries Committee. The Senate version was newly introduced by Albert Gore Jr. (D–TN).

The nearly identical bills aim to create a national policy to conserve biological diversity. Specifically, they call for creation of a National Center for Biological Diversity and Conservation Research, establishment of a federal strategy for maintaining and restoring biodiversity, consideration of biodiversity in environmental impact statements (EISs), and appropriation of $45 million during three fiscal years.

The proposed national center is to "set research priorities and provide leadership and coordination for the understanding and promotion of knowledge of the biota." Amendments added by Scheuer's natural resources subcommittee designate that the center be established within the Smithsonian Institution, to ensure its scientific integrity, and in cooperation with the Environmental Protection Agency (EPA), to tie the findings of the center to policy, in particular with the EIS process. The center is to be a semiautonomous unit of the Smithsonian and not subsumed by any existing body such as the Museum of National History.

The center would establish a cooperative network of agencies, institutions, and organizations to collect and coordinate information on the distribution, status, and characteristics of US biota for use in conservation and management. Information on communities, species, and populations that are in significant decline, of special concern, and of outstanding importance is to be compiled by the center and published by the Council on Environmental Quality (CEQ). The center would also support additional biological survey work.

The federal biodiversity strategy is to be developed by a new interagency committee working together with a new scientific advisory committee. It is to include conservation strategies on a regional ecosystem level, an approach now being implemented in the Yellowstone and southern Appalachian areas. Agencies involved would prepare, implement, and evaluate their own biodiversity plans that would include regional considerations.

Both bills further authorize federal agencies to provide partnership grants for research, management, training, and education to implement the strategy. The National Science Foundation, which is to be a member of the interagency committee, is to "provide support for research that integrates fundamental and applied science toward the conservation of biological diversity."

The sections dealing with EISs are the most controversial parts of the bills. Although witnesses before Scheuer's subcommittee agreed that loss of biodiversity is an environmental impact, it was also stated that explict directions for consideration of biodiversity are lacking. New amendments to HR 1268 direct that the EPA administrator, who is required by existing law to review EISs, shall find an action proposed under an EIS to be unsatisfactory if the action "is likely to result in a significant reduction of biological diversity." The criteria for determining what constitutes a significant reduction include losses of more than 10% of the geographic populations within any state of native species that have been found to be rare, of special concern, or in significant decline. (Separate bills reauthorizing the CEQ also direct the council to prepare guidelines for consideration of biodiversity in EISs.)

Gore's bill contains international and agricultural sections not included in Scheuer's bill for jurisdictional reasons. Representatives from agencies that work internationally are directed to coordinate their international actions with the federal biodiversity strategy. Conservation-related treaties, conventions, and educational programs should be given priority. The Secretary of Agriculture is directed to research such areas as alternative crops, integrated pest management, and native grasses.

Prospects for next year in both the House and Senate are uncertain. The House Merchant Marine and Fisheries Committee, which has written much wildlife conservation legislation, must be convinced that a new approach is necessary to enhance past actions. Scheuer's bill has 135 cosponsors, but does not yet have a majority within that committee. Gore has also assembled a bipartisan group of cosponsors.

HR 1268 has been endorsed by AIBS and most of the biological professional societies. Many environmental groups have announced their support, but they have done little lobbying so far. The extractive industries have begun to pay attention to the Scheuer bill but have not been vocal in their opposition. □

by David E. Blockstein

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Interpreting the Yellowstone Fires of 1988

Ecosystem responses and management implications

Norman L. Christensen, James K. Agee, Peter F. Brussard, Jay Hughes, Dennis H. Knight, G. Wayne Minshall, James M. Peek, Stephen J. Pyne, Frederick J. Swanson, Jack Ward Thomas, Stephen Wells, Stephen E. Williams, and Henry A. Wright

The fires that burned over the Greater Yellowstone Area (GYA) during the summer of 1988 were remarkable for their intensity and scale—the largest fire complex ever recorded for that area, the biggest in the Northern Rockies during the last half century, and one of a score of large-scale burns that have dominated the fire history of the United States during the past century (Pyne 1982). The Yellowstone fires were likewise distinctive for the intensity and scale of public and media attention given them, for the great costs of their attempted suppression, and for the timely test they provided for the management philosophies, policies, and programs of parks and wilderness areas. Also, the GYA is the site of America's first national park (1872) and its earliest national forest (1891), giving this event special significance from the standpoint of wilderness management.

The unpredictable is the essence of the wilderness experience

Several factors make the 1988 fires particularly important for wildland ecological study. In particular, the scale and heterogeneity of these fires provide unprecedented opportunities to address a variety of landscape-level questions. Furthermore, the history of research and accumulated long-term data on various components of GYA terrestrial and aquatic ecosystems will facilitate meaningful pre- and post-fire comparisons. Finally, the commitment of much of the GYA to the National Wilderness Preservation System and the designation of Yellowstone National Park as a Biosphere Reserve by the Man and the Biosphere Program of UNESCO provide an ideal setting for establishing a program of long-term research related to these fires.

The federal government inaugurated its fire protection on public wildlands when the US Cavalry assumed administration of Yellowstone National Park in 1886. In 1963, the Leopold Committee (Leopold et al. 1963), empaneled to review wildlife management issues in the GYA, recommended reformation of the policy of total fire suppression. The Park Service modified its fire policies in 1968 so that naturally ignited (lightning) fires, burning within prescribed guidelines, could be incorporated into the overall agenda of national park management.

The natural-fire management plans administered in GYA after 1972 were based on past experience and historical data indicating that fuel conditions confined large fires to old-growth pine or aging spruce-fir forests. The sheer size of the Yellowstone wilderness system was assumed to be adequate to contain natural fires. The experience from 1972 to 1988 indicated, unlikely as it now may seem, that the Yellowstone landscape was comparatively nonflammable (Romme and Despain page 695 and Schullery page 686 this issue).

In November 1988, the Greater Yellowstone Coordinating Committee (a committee of representatives from the six national forests and two national parks that comprise the GYA) assembled a panel of scientists

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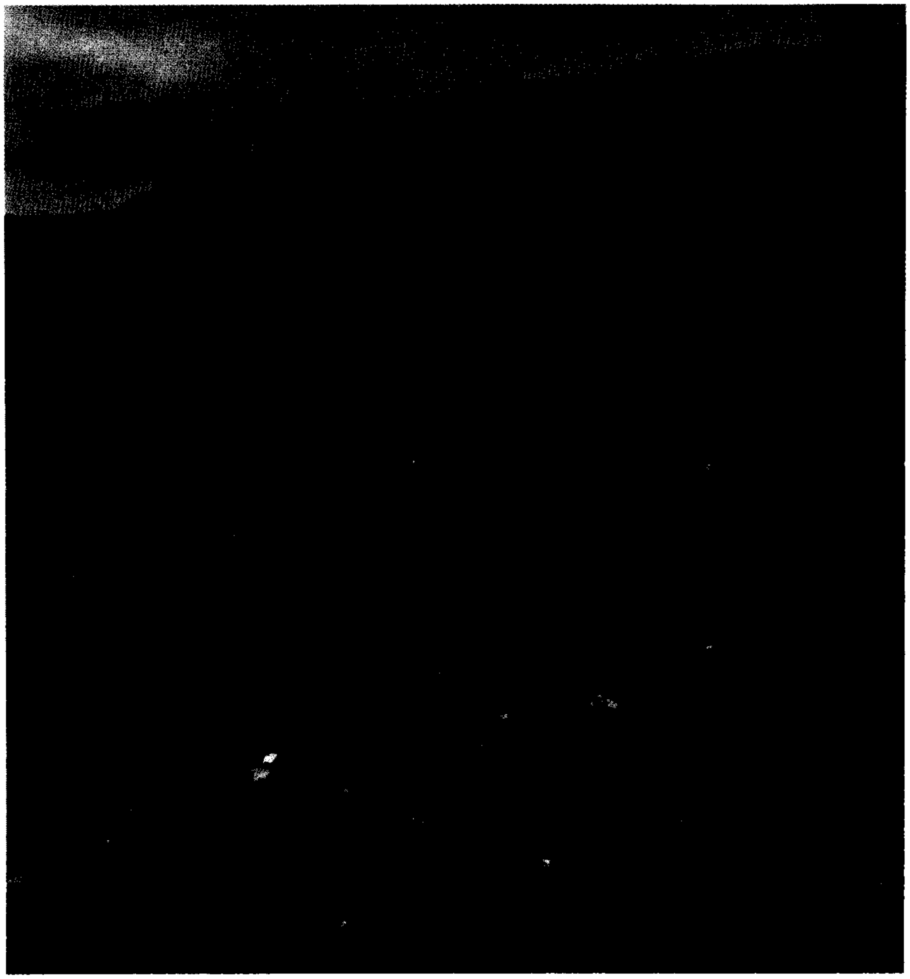
representing a wide range of ecological disciplines to consider the ecological consequences of the 1988 fires. Specifically, the panel was asked to evaluate the ecological impacts and implications of the fires in relation to watersheds, fisheries, wildlife, vegetation, soils, and biological diversity; consider the need for interventions such as reseeding (to prevent erosion), reforestation, and supplementary feeding of ungulates; make recommendations for short- and long-term research programs; and consider alternatives and options for future fire management plans. This article summarizes that panel's final report.[1]

The fires

The 1988 fires burned a total of 11% (570,000 ha) of the GYA; however, approximately 45% (400,000 ha) of Yellowstone National Park burned (Schullery page 686 this issue). The fires followed a scenario typical for the region: prolonged drought, a rash of ignitions from dry lightning storms and human sources, a steady increase in fire size and intensity through July, and a near-fire-storm climax in late August and early September. From a historical perspective, fires in fuels such as those that typify much of the GYA tend to be either small or very large. Throughout the Northern Rockies, a few fires and a few years account for most of the burned acreage (Pyne 1982). Very large fires have burned under climatic conditions less severe than those experienced in the GYA during 1988, whereas other portions of the Northern Rockies that suffered similar conditions in 1988 escaped with far less burning. In 1910, some 3.25 million acres northwest of the GYA burned according to a chronology that was remarkably similar to that observed in 1988 (Pyne 1982, Schullery page 686 this issue).

The behavior and extent of the 1988 fires appear to have been influenced more by drought and wind than by fuels. Virtually all forest age and fuel categories burned. Although precipitation was above normal in May and April, there were dramatic deficits in June (approximately 20% of normal), July (approximately 79%), and August (approximately 10%), and 1988 ended as the driest year on record. The summer drought, moreover, followed several years of below-average annual precipitation.

Abnormally strong and persistent southwesterly winds in July and August further dried fuels and caused the fires to spread at astounding rates. The size of the fires assured that they could not be stopped by small changes in microclimate, landforms, or fuel beds or by standard suppression techniques. Nevertheless, these factors did influence fire behavior on small spatial scales and contributed significantly to the resulting mosaic of burn intensities.

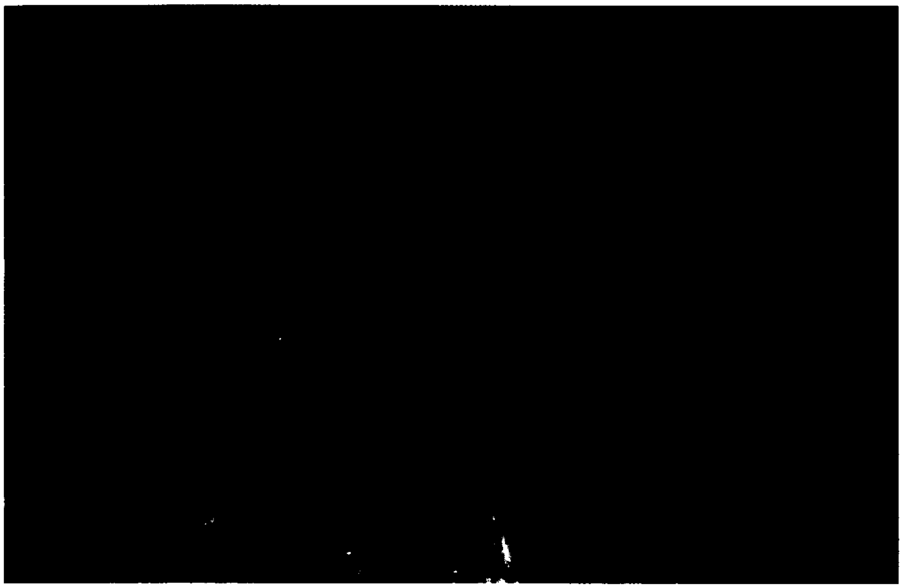


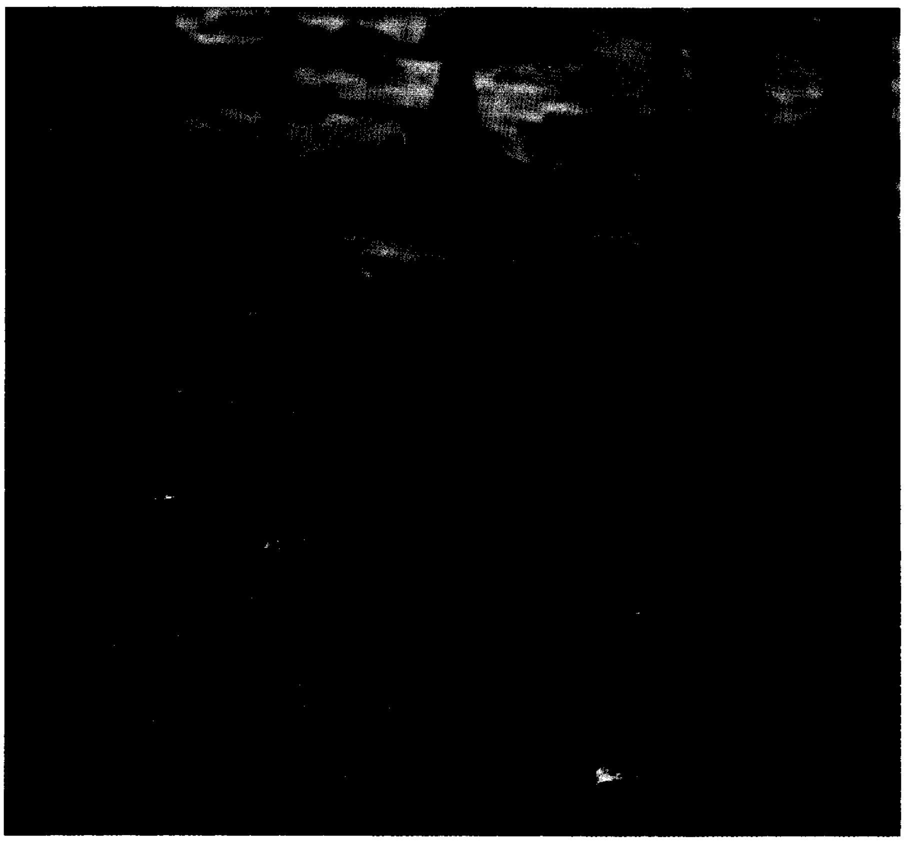
Fire mosaic on Bunsen Peak. Foreground area was also burned. View is south from Mammoth area, June 1989. Photo: Ken Spencer.

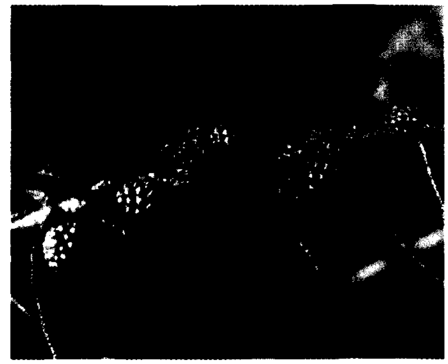
Historical data indicate that large fires follow the development of old-growth forests on a cycle of 200–300 years. The specific years in which there were outbreaks of large-scale fire probably coincided with episodic droughts (Romme and Despain page 695 this issue).

Can the scale of the 1988 fires be considered natural? That is, could such extensive burning have occurred without the influence of human activity? Romme and Despain (page 695 this issue) present convincing evidence that similarly extensive fires took place on the Yellowstone plateau in the early eighteenth century. These fires occurred before the area was settled by people of European descent and, although little is known about the impact of Native Americans, they are thought not to have increased substantially the area burned by fires. Both historically and

[1] The complete report of the Greater Yellowstone Ecological Assessment Panel, commissioned by the Greater Yellowstone Coordinating Committee of the National Park Service and USDA Forest Service to evaluate the ecological impacts of the 1988 Yellowstone Fires, is available from the Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190.







Upper left. The Wolf Lake Fire burning at night near Norris Geyser Basin, 8 August 1988. NPS photo by Jeff Henry. **Lower left.** After the fires, Yellowstone blooms again. Here, in early June, glacier lilies emerge from burned forest floor. Photo: Ken Spencer. **Above.** Some lodgepole pine cones opened after fire. The pines require fire to release their seeds. Photo: W. H. Romme.

recently, some of the fires ignited by people have burned areas that would otherwise have been burned by fires started by lightning.

Even if the scale of the fires is considered to be natural, human activities altered the pattern, and probably the specific extent, of the 1988 fires. People ignited fires responsible for much more than half the burned area. There is debate whether fuel accumulated during the century of fire suppression before 1972 increased the overall size of the 1988 fire complex (Romme and Despain page 695 and Schullery page 686 this issue).

It may not be useful to worry whether or not the fires were natural. Avoiding the influence of people may no longer be a realistic or desirable wilderness management goal. In the context of a wilderness preserve, the acceptability of events such as the 1988 fires should be judged less on the basis of their causes and more on their consequences.

Ecological impacts—knowns and unknowns

Few if any ecological processes were or will be unaffected by the 1988 fires. At least three factors will likely cause considerable variation in ecosystem responses across the GYA landscape. First, variations in fuels, winds, and terrain resulted in heterogeneous patterns of burning, causing a wide variation in patterns of plant mortality, ash deposition, and soil heating. Second, postfire climatic patterns may influence the trajectories of many ecosystem processes. Third, the prefire and postfire patterns of the landscape mosaic that affect such processes as seed rain and animal behavior may influence ecosystem responses at specific localities, independent of the direct impacts of fire at those locations. Thus, we can only phrase ecological forecasts in terms of probabilities and possibilities. The heterogeneity and spatial scale of the GYA fires provide a unique opportunity to determine how features such as site variables, vegetation, climate, and landscape mosaic interact to produce specific responses to disturbance.

Geomorphic and hydrologic responses. Fire effects on hydrology and geomorphology will be determined by spatial variations in topography, bedrock geology, soil conditions, and vegetation, as well as temporal factors, such as short- and long-term patterns of precipitation. Removal of vegetation by fire influences the relative amounts of water lost from watersheds by evapotranspiration and surface and subsurface flow (Knight et al. 1985, Knight and Wallace page 700 this issue, Swanson 1981). Increased runoff in heavily burned watersheds may result in higher peak discharges and accelerated erosion and sedimentation. Depending on factors such as fire intensity, slope, and soil characteristics, erosional processes may vary from subtle sheet erosion to catastrophic debris flows. The maximal impact of these processes could occur in the first few years (White and Wells 1981) or during several decades (Laird and Harvey 1986).

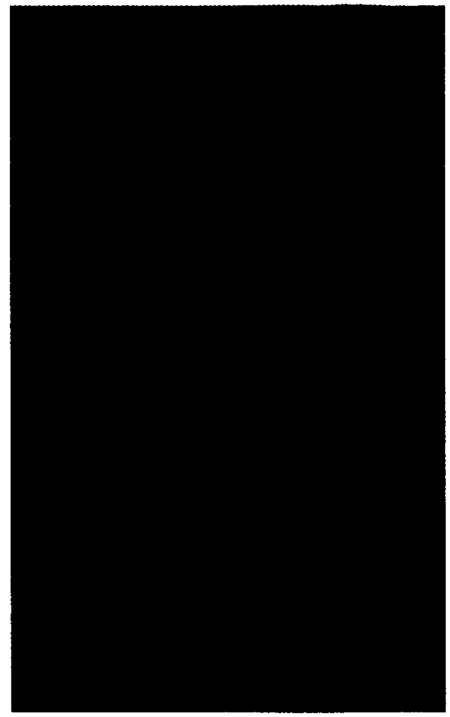
The extent, variety, and heterogeneity of the 1988 fires provide an unprecedented opportunity for a gradient analysis of watershed responses to the variety of disturbance impacts. A study of patterns of fluvial and lacustrine sedimentation in connection with studies of past fire history in the GYA would contribute a great deal to understanding the relationships between geomorphic processes and large-scale disturbance events.

Top. Ashy aftermath of crown fire, burned August–September 1988. This photo was taken in October 1988 and shows gray ash under trees. **Bottom.** Same site as above, in July 1989. The ground is now covered with *Epilobium* spp., fireweed. Photos: W. H. Romme.

Soils and belowground processes. The potential range of fire effects on soil properties is large and depends on prefire soil status, fire behavior, and postfire events. Soil heating was high (nearly complete combustion of soil litter and humus layers) only in very localized situations associated with fire storms or areas of high fuel accumulation (Shovic 1988). At these sites, loss of organic matter and depression of microbial activity may accelerate erosion and diminish fertility. However, soil heating was light to moderate at most locations, and ashfall and enhanced microbial activity probably will increase soil nutrient availability in the years immediately after the fire (Fahey et al. 1985, Raison 1979, Woodmansee and Wallach 1981).

Soil mapping projects already under way in the GYA will provide an excellent basis for studies of the factors that determine the wide range of variation in fire effects on soil processes. Because nitrogen often is limiting in GYA ecosystems (Fahey et al. 1985), the dynamics and cycling of this element deserve special attention. Little is known regarding the influence of fire on factors affecting soil water chemistry in the GYA.

Aquatic ecosystems. The immediate effects of fire on aquatic ecosystems may include increased water temperatures, altered water chemistry, and abrupt changes in food quality. Delayed impacts may include increased turbidity and sediment loading and stream channel movement. Once turbidity diminishes, conditions in most aquatic ecosystems will probably enhance production of algae, invertebrates, and fish (Minshall et al. page 707 this issue). Long-term responses of Yellowstone aquatic ecosystems will likely be closely allied with succession of surrounding forests (Cummins et al. 1983, Minshall et al. 1983, 1985). For example, recovery of for-



Aerial photos show a burn mosaic that is sometimes called a halo; patches of black, burned forest surrounded by brown, less burned areas, and by green, untouched areas. This mosaic is created by spotting (i.e., fire spread by windblown embers). See Knight and Wallace page 700 this issue for the impact of such fire on landscape ecology. Photos: Ken Spencer.

est cover will result in increased shading of streams and ponds and in decreased input of water and nutrients.

Fire effects on aquatic ecosystems probably will be greatest in small, more severely burned watersheds where thermal dispersion and chemical dilution of the water will be lowest. As larger and larger watersheds are considered, greater percentages of the area will not have burned, and the larger catchment will diminish the effects of the fire.

The scale and heterogeneity of the 1988 fires provide unique opportunities to develop models of the relationships among physical, chemical, and biotic features of aquatic systems and patterns of disturbance. Studies should include evaluation of sediment and nutrient pulses in both fluvial and lentic ecosystems. Studies to measure the extent to which riparian and wetland features buffer stream-water chemistry or act as nutrient filters will provide an ideal opportunity to investigate the coupling of aquatic and terrestrial ecosystems.

Patterns of plant succession. The importance of past fires in shaping vegetation patterns in the GYA is clear (Romme and Despain page 695 this issue). Certain adaptations to fire seen in many native plants (e.g., the serotinous cones of lodgepole pine) testify to the long-term role of fire as an evolutionary force on the GYA landscape. Thus, in most locations, regrowth will be rapid.

The total number of possible permutations of successional pathways on the Yellowstone landscape is large. Successional change at any location will depend on such factors as fire intensity and size, seed availability, abundance of sprouting growth forms, topographic and soil characteristics, preburn vegetation structure, and climatic conditions in the next few years (Knight and Wallace page 700 this issue, Romme and Knight 1981, Stahelin 1943). Landscape diversity could be enhanced where the mosaic of successional patterns is superimposed on the burn mosaic and as the process of successional change continues in the forests that were not burned in 1988.

The effects of the fires on Yellowstone plant communities of the next few decades are expected to include: a larger area in meadows and young forests; aspen forest over a larger area, though probably still a small portion of the park; sagebrush, because of its inability to resprout after fire, will be less abundant in some areas for a decade or more; and more luxuriant herbaceous vegetation for several decades (Knight and Wallace page 700 this issue).

Biodiversity. The importance of natural disturbance processes such as fire in the maintenance of landscape diversity in the GYA has been thoroughly documented (Houston 1973, Patten 1963, Romme 1982, Romme and Despain page 695 this issue). No species is known to be threatened as a consequence of the 1988 events, although the relative abundances of species will probably change. The increased spatial variability in environment and varied patterns of postfire recovery will likely enrich species diversity (Taylor 1973). Decreased expanses of contiguous old-age forest may result in the diminished abundance of interior forest species. However, species favoring edges and those requiring two or more habitat types can be expected to increase in abundance (Franklin and Forman 1987). An unwanted increase in diversity of alien species, especially noxious weeds, could occur in some locations (Weaver and Woods 1985).

The preservation and management of large mammals have been important issues in the GYA for decades (Chase 1986, Leopold et al. 1963). The direct and indirect effects of the 1988 fires on ungulate populations are described by Singer (page 716 this issue). Although the combination of drought, reduction of winter range by fire, and the harsh winter immediately following the fires may reduce ungulate populations, improved forage quantity and quality should enhance survival, growth, and fecundity during the next several years (Boyce in press, Houston 1982, Singer page 716 this issue).

It is tempting to suggest that the Yellowstone landscape has been restored to some state that existed hundreds of years ago. However, the data are insufficient to support such an assertion. We can state with confidence that events similar to those of 1988 have altered GYA ecosystems in the past (Romme and Despain page 695 this issue). Still, the Yellowstone of 2072 will not be the same as that of 1872, just as the landscape of 1872 was unique compared with previous times. Even without human influences (of which there have been many; Haines 1977), Yellowstone landscapes would continue to change if for no other reason than climatic changes and the continued evolution, immigration, emigration, and even possible extinction of plant and animal species. Big changes occurred in 1988, and it is safe to assume that such changes will occur again in the future. Indeed, such change is the *sine qua non* of wilderness.

Postfire management interventions

Artificial feeding of ungulates (e.g., deer), seeding with short-lived alien herbs in areas subject to erosion, and artificial reforestation activities to speed ecosystem succession are among the postfire interventions thus far proposed by some groups. However, there are compelling arguments for a light hand in coping with the unique scene created by the fires of 1988.

The borders of wilderness preserves have for the most part been defined on the basis of political and economic criteria, with little or no regard for natural divides or ecological boundaries that regulate natural processes. The consequences are reciprocal: an event outside wilderness preserves can affect ecosystems within and events within wilderness ecosystems can reach outside the preserves. Where the potential impacts on nonwilderness ecosystems are great, artificial interventions may be required. Nevertheless, interventions that diminish wilderness values should be pursued only if a threat to nonwilderness ecosystems is clear and only if it is reasonably certain that such interventions will achieve their intended goals.

Feeding. Artificial feeding programs are expensive, alter animal behavior, facilitate spread of disease, and often do not work. Worse, such programs focus attention on single components of ecosystems, especially the charismatic megafauna (e.g., bison, elk, and bears), and reflect an unwillingness to recognize that natural processes in wilderness ecosystems often have results that in human terms appear to be cruel. Wilderness preserves should not be managed as either zoos or museums, item by item. Rather, the goal is to preserve the complexity of dynamic interactions among the various ecosystem components that are essential to its functioning.

Soil stabilization. The erosion processes that shape wilderness landscapes do not operate at constant rates, but rather they occur in episodes associated with natural disturbances such as fire. The 1988 fires probably will alter runoff and increase erosion in many locations on the Yellowstone landscape. Within the context of wilderness, such changes are expected and in some cases even desirable. The geomorphologic and hydrologic consequences of the Yellowstone fires certainly are legitimate concerns for nonwilderness ecosystems downstream. However, the potential impacts currently do not appear to be sufficient to warrant an emergency soil stabilization program, if indeed one were possible across such a large area. Remedial measures such as seeding with alien species may temporarily stabilize soils, but in the long term they could actually accelerate erosion by interfering with establishment of native plants and encouraging their replacement with noxious weeds.

Reforestation. Other proposed remediations, notably artificial reforestation, should be evaluated according to whether or not the lands are managed for wilderness values. In lands dedicated to commercial forestry or adjacent to human developments, there may be a case for reforestation activities. But in acknowledging fire as an integral process of natural ecosystems, we must also accept the natural processes of postfire ecosystem change as an integral part of wilderness landscapes. Nearly all native species in these ecosystems are adapted to or depend on fire in one way or another. The specific patterns that emerge will depend on such factors as prefire ecosystem structure and species composition, specific site environments, local patterns of fire severity, and unpredictable postfire events including year-to-year variations in climate. This combination of variables was responsible for much of the variety of the Yellowstone landscape before the 1988 fires and will undoubtedly contribute to the future heterogeneity of that landscape. It would be difficult, if not impossible, to devise a reforestation strategy that could replicate this diversity. Furthermore, artificial planting probably would alter the distribution of tree genotypes.

Research philosophy

If prudence argues against aggressive intervention, it also argues against a doctrinaire strategy of laissez-faire. It would be reckless and irresponsible to commit irrevocably to a particular management strategy when the scale of the disturbance involves half the park wilderness and the future pathways of landscape change are known only within broad parameters. If our state of knowledge argues against emergency intervention, our state of ignorance argues for a program of aggressive data collection and evaluation. A monitoring network adequate to gauge postfire changes simply must be present to compare actual developments with forecasts and thereby make informed judgments. In order to thrive, a monitoring program must complement an active agenda of scientific research.

Because of the location and scale of the 1988 fires, tremendous public and scientific interest now centers on the GYA. The 1988 fires provide the opportunity to study disturbance at the landscape scale, in an area that has not been heavily influenced by humans and in a context that should facilitate the establishment of long-term studies. The challenge is to focus these resources on important research issues and to organize a program that can follow through with long-term observations that are essential to interpreting the ecosystem consequences of the fires. Success requires substantial and rapid agency commitment.

The three essential ingredients of a research program for events such as the GYA fires are an ecosystem approach to provide for conceptual integration and operational coordination of many research projects, a landscape or geographic context for individual projects, and provision for long-term studies and monitoring of key system characteristics and processes. The ecosystem approach will facilitate coordination of projects, which increases opportunity for serendipity and synergism and increases the efficiency of investment in basic environmental monitoring (e.g., climate and streamflow) needed to support such studies. Understanding and recognizing the geographic context of research sites is necessary to extrapolate observations over larger areas based on information such as the burn severity maps.

The 1988 fires will have ecological consequences that extend over a century or more. Therefore, it is important to establish research programs that deal with the long-term aspects of these processes.

Management implications

Federal wilderness preserves are administered within a matrix of legislative mandates, agency directives and policies, and locally prescribed policies and protocol. Elements of this matrix both proscribe and prescribe certain actions, but they do not dictate a single, monolithic scheme in all preserves. Management ambiguities often result. Fire management programs within individual wilderness preserves do not follow as a syllogism from national policies and handbooks. The need to allow for local discretion and to accommodate local situations perpetuates rather than removes these ambiguities and uncertainties. Yet too often guidelines assume more knowledge than is actually available and policies assume consensus where there is conflict.

We have learned enough to know that wilderness landscapes are not predestined to achieve a particular structure

Fires on the scale of those in Yellowstone demand decisions, but they also distort and magnify inevitable flaws in protocols for making such decisions. When fires of a magnitude such as those observed in 1988 occur in a place (such as Yellowstone) that can attract major media attention, they take on the character of a celebrity scandal.

Humans often can intervene with fire in ways that they cannot intervene with volcanoes or hurricanes. We can apply or withdraw ignition, and we can reshape the environment within which a fire may burn. Both fire suppression and prescription, however, pivot on a paradox. The only way to eliminate wildland fire is to eliminate wildlands. To extirpate fire completely from a wildland ecosystem is to remove an essential component of that wilderness. Similarly, to alter the fuels in a significant way is to change the character of the wildlands that are being protected. The strategy has thus evolved to substitute various kinds of controlled or prescribed fire for wildfire. Designating naturally ignited fires as prescribed fires (or as confined suppression fires) belongs within this spectrum of management options.

When, following the Leopold Report (1963) and the Wilderness Act (1964), the dilemma of fire protection in wilderness and parks became an object of intense scrutiny, many observers believed that wilderness fire management involved merely the restoration of a natural process into a natural environment. The required means were conceptual conviction and political will. In its purest expression, a wilderness fire program sought to withdraw suppression practices and permit naturally ignited fires to burn freely. Since then, the philosophical issues have blurred and the operational problems have multiplied. It is not enough to withdraw aggressive suppression from wild areas. Rather, fire management must blend various forms of suppression with various forms of prescribed fire.

Fire programs must necessarily be predicated on a state of knowledge that is fallible and a capacity for environmental control that is imperfect. It is unwise for fire agencies to claim perfect knowledge, and it is unfair for the public to demand it of them. It is not necessary that all specific outcomes of fire programs be known in advance, only that a program be able to specify an acceptable range of outcomes and identify the means by which fire can achieve them.

Fire management on public lands now operates under a pluralistic policy that allows in principle for an equilibrium between fire use and fire control. Within the decision to suppress fire, a number of responses are possible. The Yellowstone fires do not so much challenge the wisdom of that policy as they demand the support necessary to implement it. Fire management plans must include, in the context of detailed written prescriptions, guidelines for monitoring and evaluating natural prescribed fires. Presuppression plans to guide major fire-control operations are essential. Care must be taken that interagency agreements to harmonize procedures for accepting fires along administrative borders do not disguise different operational criteria for distinguishing between prescribed and wildfires. Also, the acceptability of naturally ignited fires must be conditioned by the constraints of preserve design and size. Fires that might be considered natural by various criteria will not necessarily be acceptable in the context of such constraints.

It is clear that the assortment of fire management plans in the GYA was inadequate for the 1988 fires. However, it is unlikely that any fire plan could have foreseen an event of this magnitude or coped with a complex of fires that, by the time the decision to suppress was made, was uncontrollable (Schullery page 686 this issue).

Once a fire becomes large, suppression is often possible only when the weather changes.

Increasingly, wilderness management has emphasized the preservation of natural processes rather than simply the preservation of natural features, objects, or scenes. We now recognize the subversive consequences of halting natural succession and the futility of trying to recreate a former scene over large areas. Even if knowledge of former circumstances was perfect, which it is not, social, climatic, and environmental conditions have changed so much that an ideal replication is unlikely. The landscape embodies chance as well as mechanism; there are those who would argue that chance is itself a value, that the unpredictable is the essence of the wilderness experience.

Knowledge of the causes and consequences of natural processes such as fire is rudimentary, but we have learned enough to know that wilderness landscapes are not predestined to achieve some particular structure or configuration if we simply remove human influences. A great variety of future natural landscape configurations is possible, although all configurations are not equally likely nor equally desirable. Given the restricted size and arbitrarily defined boundaries of most wilderness preserves, some possible configurations may be far less desirable than others. We cannot escape the need to articulate clearly the range of landscape configurations that is acceptable within the constraints of the design and intent of particular wilderness preserves.

It is easy to promulgate objectives to protect and preserve a particular scene in wilderness preserves, but developing analogous objectives to preserve and protect particular natural processes have proven considerably more difficult. It is clear that, just as human presence in and around wilderness landscapes is inescapable, human intervention and manipulation will be necessary to preserve those processes. The questions that the next generation of natural area managers must address are not whether manipulations is desirable, but what kind of manipulation is acceptable? By what means? For what purposes? On what scale? According to what social and political processes? They must rewrite ideals into management objectives and develop and install monitoring procedures adequate to measure progress toward those objectives. Most important, they must actively support research programs that reduce the state of uncertainty regarding the natural phenomena they are charged with managing.

While accepting that chance exists in the natural world and that management is required even when knowledge is incomplete, managers must also recognize that it is possible to narrow the choice of purposes, to contract the range of ambiguity surrounding objectives, and to shrink the domain of ignorance. Many unknowns can be reduced to uncertainties, and uncertainties to probabilities.

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The Fires and Fire Policy

The drama of the 1988 Yellowstone fires generated a review of national policy

Paul Schullery

The Greater Yellowstone Area (GYA) fires of 1988 were, in the words of National Park Service (NPS) publications, the most significant ecological event in the history of the national parks (NPS 1988). Their political consequences may be as far-reaching as their ecological consequences.

The fires have been characterized in many ways, from natural catastrophe to ecological wonder and from policy blunder to scientific bonanza. They have generated a national dialogue that goes beyond the issue of fire in national parks and forests to more fundamental questions about the management of public lands.

The term *Yellowstone fires* is an unfortunate oversimplification. The fires occurred in the GYA, 4.8 million ha of mostly public land in Wyoming, Montana, and Idaho. The GYA consists of Yellowstone (YNP) and Grand Teton National Parks (GTNP), two national wildlife refuges, and six national forests, as well as state and privately owned land (GYCC 1987).

Fire management history

Ecologists have long recognized that fire was a major factor shaping landscapes in prehistoric America. Fires set by lightning or American Indians controlled plant and animal communities in most North American settings. Fire was a tool for land management among many early European settlers as well, for clearing land and encouraging the growth of preferred plants and animals (Pyne 1982, Wright and Bailey 1982).

It is difficult to separate scientific interest and aesthetic wonder from consternation at the political effects

Early in this century, the course of federal fire management was largely a reaction to some huge and economically disastrous forest fires. For example, in 1910, fires burned 3 million acres in Idaho and Montana, mostly on government land, destroying several towns and killing dozens of fire fighters. Therefore, fire management was regarded simply as fire suppression (Pyne 1982). In the 1940s, however, the US Forest Service (USFS) began to use fire as a silvicultural tool in some southeastern forests (Kilgore 1976). In the 1950s, the NPS started experimenting with controlled burns in Everglades National Park. Similar experimentation was conducted in Sequoia National Park in the early 1960s, and by 1972 there were 12 NPS areas in which some lightning-ignited fires were allowed to burn (Kilgore 1985, Parsons 1981).

For the NPS, allowing natural fires to burn was only part of a broad management redirection. The initial impetus for redirection was the 1963 Leopold Report, named for A. Starker Leopold, chairman of a committee of ecologists appointed by the secretary of the interior to consider wildlife management issues in the parks (Leopold et al. 1963). The committee proposed that the highest goal of the parks was to maintain "biotic associations" that were found in the park area when first visited by Europeans. Where such associations could not be maintained or recreated, a "reasonable illusion of primitive America" could at least be kept in place.

This charge, which became NPS policy in 1968, was fraught with complications. No national park is ecologically isolated from its surroundings; little is known about the precise ecological condition of any park at the time it was first visited by Europeans; maintaining biotic associations requires maintaining dynamic natural systems in which change is unavoidable, thus precluding the maintenance of any specific ecological state; natural systems cannot change without affecting the relative abundance of various elements of the biotic communities; and elements of the pre-European setting, such as American Indians, may no longer be present, nor may their effects be known or replicable. The Leopold Committee and many subsequent observers recognized these complications, but respecting parks for their ecological processes was widely recogized as a

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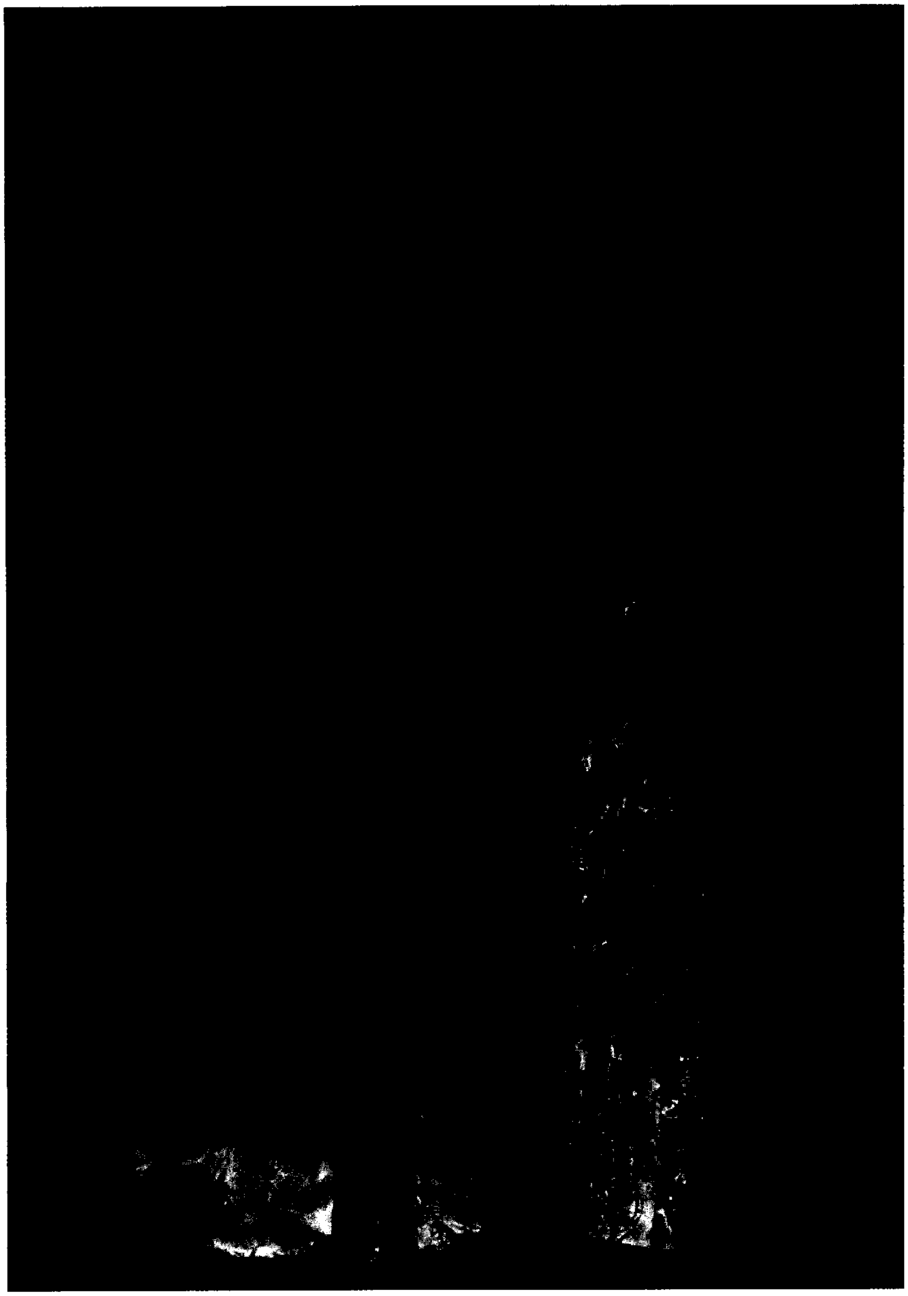
useful ideal around which management policies have evolved (Houston 1971). YNP has been a pivotal and controversial testing ground for the Leopold Report, and the fires of 1988 may have provided the sternest test of the practicality of maintaining biotic associations.

Of management agencies in the GYA, the NPS has recently pursued a natural fire policy most aggressively. From the establishment of the park in 1872 until 1971, all fires were fought as well as personnel and equipment permitted (Houston 1973, Taylor 1974). Fire suppression, however, was not consistently effective in the park's extensive forests until the arrival of aerial fire fighting technology after World War II (Romme and Despain page 695 this issue and Schullery and Despain 1989). In 1972, 15% of the acreage of YNP (136,000 ha), all in backcountry areas, were designated as natural fire zones. Any lightning-caused fires starting there were to be allowed to burn, if they did not threaten human life, property, cultural sites, or specific natural features of unusual value, such as threatened or endangered species (Despain and Sellers 1977, NPS 1987). Although the policy also allowed park managers to intentionally ignite fires, a procedure used freely in some other parks, it was not considered useful by Yellowstone managers because climate, rather than available ignition sources, seems to be the driving force behind fire's effect on the Yellowstone landscape (Romme and Despain page 695 this issue). During the next several years, most of the park was added to the natural fire zones (NPS 1987). GTNP initiated a similar plan in 1972.

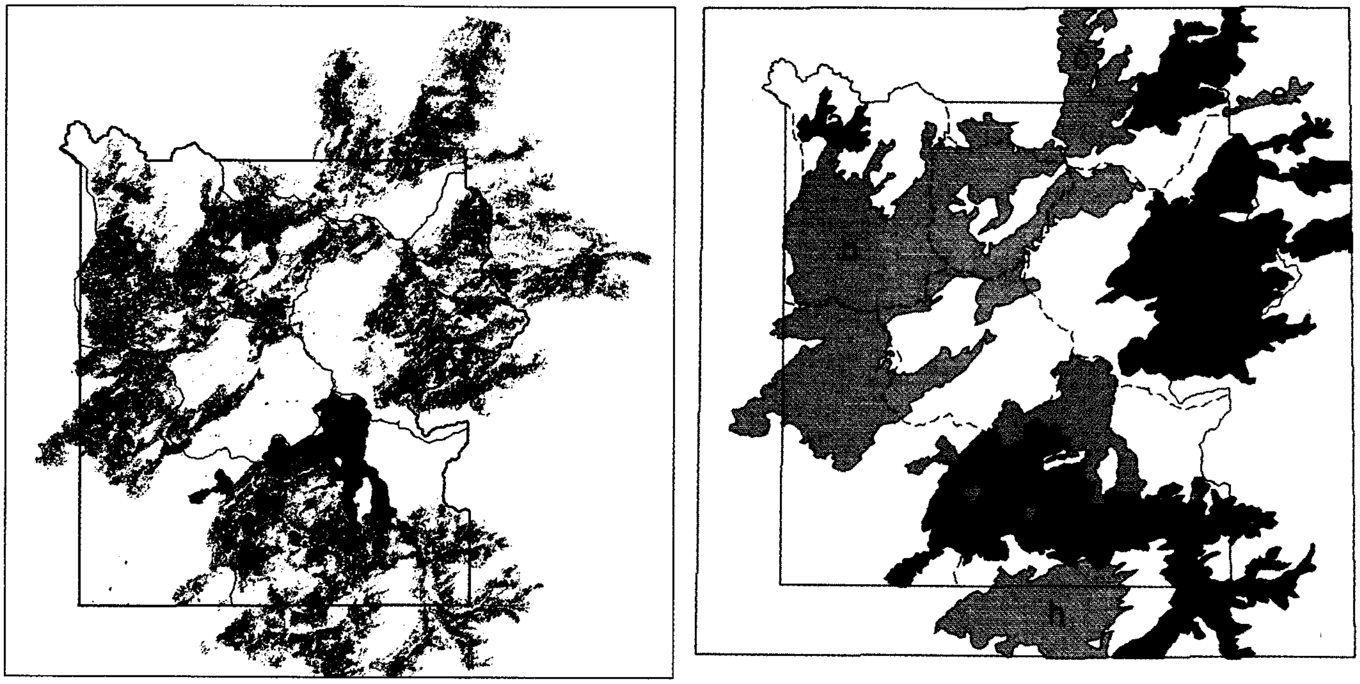
The national forests surrounding Yellowstone Park also developed natural fire management plans, and cooperative agreements that were in place by 1988 allowed managers in a park or forest to "accept" a fire that was approaching their boundary from another unit (USDA/USDI 1988). There were substantial differences in the plans of the parks and forests, especially in their arbitrarily prescribed limits on the size to which a fire might be allowed to grow; NPS plans accomodated large fires, whereas USFS plans were more restrictive because those areas are being managed to meet a different mandate.



Scenes like this one were common on the TV evening news. The fire is part of a back burn set just inside the northeast corner of Yellowstone National Park as part of the fire suppression efforts on the Storm Creek Fire, Labor Day weekend, 1988. NPS photo by Jim Peaco.

Newcomers to the fire dialogues may find the language puzzling. In fire management, a *prescribed fire* is one that, whether it was set by humans or lightning, is burning within the prescriptions set by managers for fires that will be allowed to burn, sometimes for months. In YNP, virtually all prescribed fires are lightning-caused. A *wildfire* is a fire that does not meet the agency's prescriptions. A prescribed fire can behave in such a manner that it is reclassified as a wildfire. But a wildfire is not necessarily one that is out of control; it is merely a fire that must be suppressed. Thus, almost counterintuitively, a wildfire is often a human-set fire and a prescribed fire is generally caused by lightning.

In its first 16 years (1972–1987), the Yellowstone Fire Management Plan was widely considered a success within the agency and among conservation groups. In that period, 235



Left. What burned in the Greater Yellowstone Area. Key to map: red, crown fire in dense forest; green, mixed dense vegetation; orange, crown fire in medium-density forest; turquoise, mixed medium-density vegetation; yellow, crown fire in sparse forest; light green, mixed sparse vegetation; dark green, nontimber burn. **Right.** Major GYA fires by ignition source. Key to map: pink, human-caused; green, originating on US Forest Service land (natural); orange, originating on National Park Service land (natural); blue, lakes. **a.** Fan Fire. **b.** North Fork Fire. **c.** Hellroaring Fire. **d.** Storm Creek Fire. **e.** Human-caused burn, set as part of Storm Creek Fire control efforts. **f.** Clover Mist Fire. **g.** Mink Fire. **h.** Huck Fire. **i.** Snake River Complex Fire. Maps produced by the Geographic Information Systems Division, Yellowstone National Park. Data gathered and analyzed by Don Despain, NPS.

fires were permitted to burn a total of 13,662 ha (NPS 1987). Only 15 of the fires exceeded 40 ha, and all the fires extinguished naturally. The largest single fire burned 2960 ha. Public education programs by the NPS stressed the values of restoring fire to its place in wilderness processes, and public acceptance of the program was perceived as high.

The small size of most fires indicated that in a typical summer, though there will be hundreds of lightning strikes, few will result in fires of any size. The lodgepole pine (*Pinus contorta*) forests that dominate much of the GYA (and constitute 77% of YNP forests) do not burn easily and have little undergrowth until old age (Brown and Bevins 1986, Romme and Despain page 695 this issue). Only the oldest forests—those with substantial fuel in downed trees and undergrowth—burn readily. During 1972–1987, fires were regularly observed to skip over, pass around, or stop at the edge of young forests.[1]

[1]Don Despain, 1989, personal communication. Research Division, National Park Service, Yellowstone National Park, WY.

Dendrochronological research suggested that the process by which Yellowstone's mosaic of vegetation types was maintained did not operate consistently, year by year. Instead, GYA forests appeared to alternate between short periods—a year or a few years—of large fires and long intervals (200 to 400 years) of relatively small fires each year (Romme 1982). By 1988, it was clear that the GYA had in the past experienced very large fires and also that extensive areas of the park were entering their most burnable stage. Roughly one-third of the park's forests were 250 to 350 years old (Romme and Despain page 695 this issue). The advanced age of many forests seems to have been a much more significant factor in the accumulated fuel loads than any effects of human fire suppression since the establishment of YNP in 1872 (Schullery and Despain 1989).

The 1988 fire season

The GYA entered a mild drought late in 1987 and was considered to be in a severe drought by mid-May (USDA/USDI 1988). The GYA climate is typified by dry summers; most precipitation falls as snow (Dirks and Martner 1982). But in the period from 1982 to 1987, the GYA experienced an average of about 200% of normal precipitation in July (NPS 1988). Although much of the west suffered a serious drought in those years, naturally caused fires burned less than 400 ha in the park during those six years. Fire managers began to anticipate the continuation of wet summers, and April and May of 1988 seemed to herald yet another wet season.

But in the spring, a high-pressure zone formed and settled over the northern Rockies as the jet stream sent incoming storms north into Canada. Fuel grew progressively drier, and frequent thunderstorms provided lightning but no rain. The summer was the driest in the park's recorded history. In August and September, a series of six dry cold fronts crossed the GYA, bringing winds that routinely gusted 60–100 km/hr (USDA/USDI 1988). Within this extraordinary climatic context, the GYA fires ignited and grew.

By the standards of the previous 16 years, the 1988 fire season began routinely. In late May and early June, 11 of 20 early season fires extinguished naturally, and the rest exhibited no unusual behavior. NPS and USFS fire specialists monitored the fires and a variety of recognized danger indices, including moisture content of fuels, lightning- and man-caused fire risks, energy release component (the heat given off by a fire dictates how it will be fought and what equipment must be on hand), and spread component (a computation of probable speed of a fire's movement based on conditions).

The first three weeks of July are the critical period in the early stages of the fire season. Managers watched fire conditions with growing concern, then alarm, even though the fires were not yet especially large. On 15 July, for example, only approximately 3440 ha had been burned in the entire GYA. On 21 July, when NPS personnel decided to declare all fires wildfires and suppress them, 6800 ha had burned. By then the fires were national news, and on 27 July the secretary of the interior visited the park and reaffirmed the decision to fight all current and new fires there (Figure 1).

But by then continued dry weather and high winds had pushed the park across the threshhold for large fires. Within a week of the decision to suppress all fires, the perimeter acreage of YNP fires exceeded 40,000 ha. By 15 August, the perimeter total was approximately 100,000 ha. By 1 September, the GYA total was 340,800 ha, with 220,000 of that in the park. These preliminary estimates were often based solely on helicopter overflights; detailed mapping of burn areas is still under way. All burn area figures that follow in this article are based on aerial mapping with a resolution of 80 ha; later-generation maps are expected to reduce most burn area figures as the burn mosaics are plotted more precisely.

There were 248 recorded fire starts in the GYA in 1988, 31 of which were allowed to burn as prescribed fires. Twenty-eight of the 31 were in YNP. Seven fires were responsible for more than 95% of the area burned (Maps, page 688). Five of those seven originated outside YNP, and three of those five, including the largest fire of all (the North Fork Fire, 201,610 ha), were human-caused wildfires fought from the start (Figure 2).

Satellite image of Wyoming-Montana-Idaho-Utah-Colorado area on 7 September 1988 shows major smoke plumes from Greater Yellowstone Area fires spreading across Wyoming, while smaller fires burned in Montana, Idaho, and Utah. Photo: NASA/Ames Research Center.

The scale of the fires shocked many people. On the much-publicized "Black Saturday," 20 August, wind-driven flames burned 64,000 ha. Smoke and particles from the GYA fires traveled east across North America, sometimes obscuring the sun for hundreds of kilometers. Some of the fires deliberately set by fire fighters to deprive an oncoming fire of fuel were larger than most natural fires of the previous 16 years.

Fighting the fires

On 23 July, GYA managers created the Greater Yellowstone Area Command, located in West Yellowstone, Montana, to coordinate fire-fighting operations in the GYA. As the fires grew, resources from other agencies and regions were drawn into the effort. Approximately 25,000 fire fighters participated during the course of the fire season, as many as 9500 at one time. On many occasions, there were not enough fire fighters or equipment to attack all fires fully. Fire fighters from land management agencies were aided by personnel from the Wyoming National Guard and the Air National Guard and the US Army, Air Force, Marine Corps, and Navy. More than 100 aircraft and 100 fire trucks from several states also were used. The total cost was approximately $120 million.

Fire behavior was characterized as "unprecedented" by many sources, but it would be more precise to say that fire in the GYA had never been experienced on such a grand scale. Previous fires in North America had burned as much or more acreage and had behaved as spectacularly, but not in the presence of what was probably the largest single fire suppression effort in American history or in the face

Satellite image of the North Fork fire approaching the town of West Yellowstone, MT, on 2 September 1988 (top is north). Note numerous spot fires appearing along the leading edge of the westbound fire. The river is the Madison, which leaves the park just north of West Yellowstone and eventually becomes one of three rivers that join at Three Forks, MT, to form the Missouri River. Notice that the west boundary of Yellowstone National Park is clearly delineated south of West Yellowstone. Clearcuts in Targhee National Forest show differences of land use directions among various elements of the Greater Yellowstone Area. Photo: NASA/Ames Research Center.

of such advanced knowledge of fire behavior.

Fires advanced as much as 16 km in a day. Wind-driven flames routinely jumped formidable barriers, such as the Grand Canyon of the Yellowstone River, park roads, and even the broad expanse of the Upper Geyser Basin. When winds carried embers ahead of the fire's front, spot fires were created as much as 2.5 km in advance of the main fire. These spot fires complicated efforts to fight fires head-on; fire fighters were in danger of becoming trapped between the main fire and its outlying spot fires.

Fast-moving fires were impossible to stop with conventional hand- or bulldozer-dug trenches (fire lines). Fire jumped most of the hundreds of kilometers of fire lines that it approached. Because of the extreme volatility of fuels and low relative humidity, fires did not stop moving at night as they often do; fire fighters could make no more progress at night than in the day (USDA/USDI 1988). Attempts to project maximal possible size of a given fire were repeatedly foiled.[2]

Yellowstone attractions added unusual hazards. All fire camps had to be kept clean to avoid conflicts with grizzly bears (*Ursos arctos*) and other scavengers, and some fire fighters were injured when they inhaled fumes from burning mineral deposits near hot springs. Fire fighting focused most effectively on protection of developed areas. Although the fire-fighting effort may not have significantly reduced the total acreage burned by the large fires, fire fighters were successful in protecting buildings. In a series of dramatic stands, several park developments and surrounding communities were saved by such techniques as intensive fuel reduction along their edges and the soaking of buildings with water and fire retardant (Figure 3).

The most famous episode was the Old Faithful fire storm of 7 September, when the eastbound North Fork fire, driven by winds in excess of 100 km/hr, jumped over the entire 400-structure development, the Firehole River, and the Upper Geyser Basin. Twenty-two small buildings, mostly cabins, were destroyed, and several others were damaged; these losses were considered light under the circumstances. A total of 67 structures were destroyed in the GYA, and another 12 were damaged.

There were numerous, mostly minor, injuries to fire fighters. However, one fire fighter was killed by a falling snag in October operations on the Clover-Mist fire in Shoshone National Forest, and a pilot was killed when his light plane crashed near Jackson, Wyoming.

Fire-suppression impact

The impact of the fire-suppression efforts will be visible for many years. Dozens of camps and helicopter landing sites were scattered through the GYA. Approximately 1071 km of hand-dug fire lines and 220 km of bulldozer lines were also constructed. After September, precipitation quieted the fires, and fire crews worked to minimize the effects of these disturbances. However, the turning of the soil may result in increased erosion, heightened hospitality to nonnative plants, or simply an enduring scar. Removal of trees creates an artificial corridor that will remain apparent indefinitely (Figure 4).

Fire-fighting activities can displace wildlife (as when a camp is built in a meadow where animals graze) or attract it (as when food is brought into bear country). Collisions with fire-fighting vehicles killed 108 large mammals, but such collision mortality is typical of YNP in other summers. Fire trucks and other vehicles often drove off roadways, some as far as three miles; these scars may last 30 or more years. Aircraft logged more than 18,000 hours of flight time in YNP alone (Figure 6). The noise of the aircraft, especially at helicopter landing strips, displaced animals, but no formal monitoring was undertaken due to the emergency situation.

Approximately 5.3 million liters of fire retardant were dropped on fires in YNP. This retardant may have short-term fertilizing effects on vegetation; but at least two small fish kills, approximately 100 fish each, resulted from retardant drops in streams. Thirty-eight million liters of water were dipped or pumped from various GYA streams and lakes for dumping on fires, drawing down some ponds and disturbing natural processes in many others (Figure 5).

Assessing ecological impacts

Aerial mapping of GYA fires was completed in September 1989 (GYP-FRAC-BAST 1988). According to this preliminary coarse-resolution mapping, fires affected more than 560,000 ha—395,570 ha of which were in YNP (Table 1). Fires burned with varying intensity and effect. In the GYA, 61% of the burned area experienced canopy burn (trunk, limbs, and needles or leaves of trees burned), and 34% experienced surface burn (fire crept along the ground and did not burn the canopy, leaving many trees partly or completely unburned). An additional 32,000 ha of meadows and sage grasslands were burned

[2]Richard Rothermel, 1989, personal communication. Intermountain Research Station, USDA Forest Service, Missoula, MT.

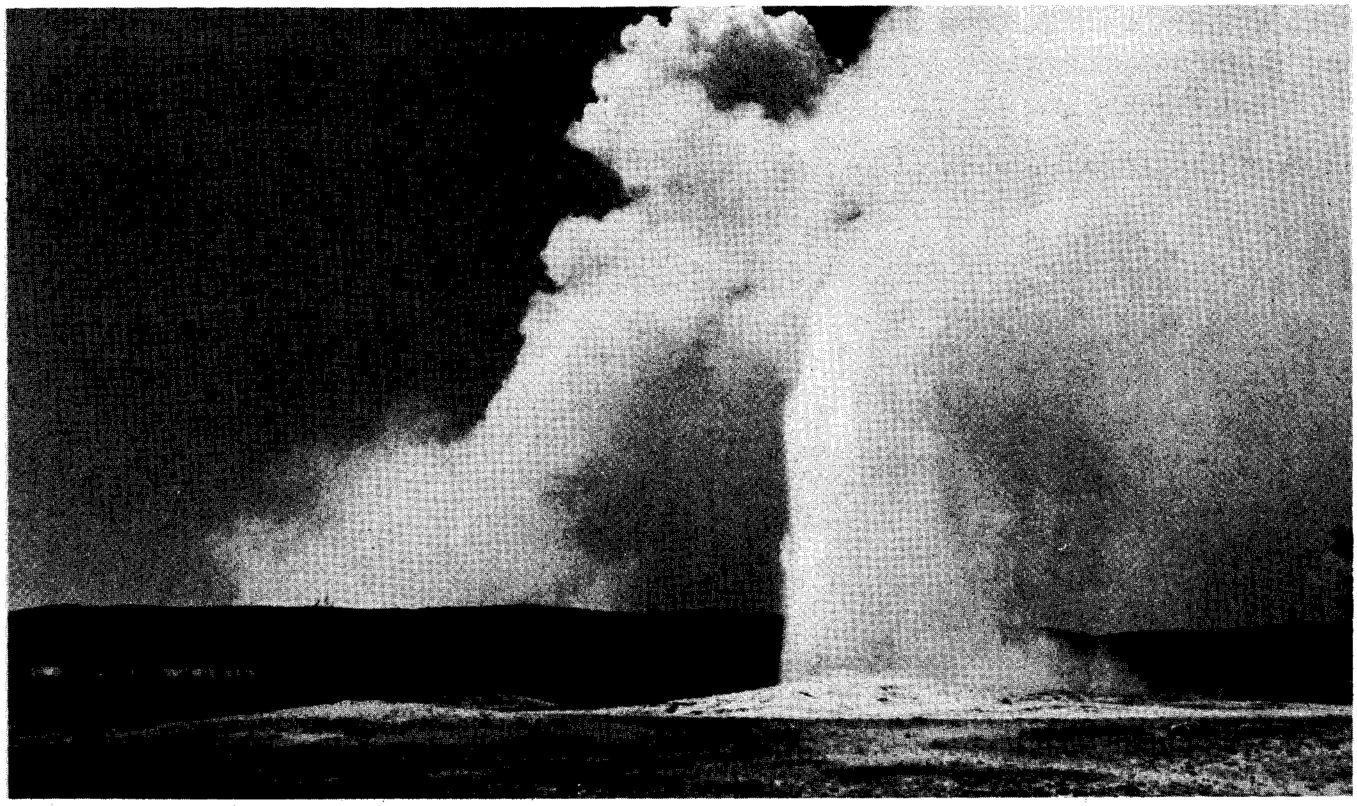


Figure 1. The North Fork Fire's smoke was visible at Old Faithful on 25 July 1988. Photo: Jim Peaco, National Park Service.

(GYPFRAC-BAST 1988).

The result of the varying burns is a mosaic of burned, unburned, and partially burned areas. There is little uniformity of pattern or scale across the mosaic; fires were influenced by many factors, including wind, slope, fuel availability and condition, and humidity, so that in some areas the mosaic is quite fine (with burned and unburned patches only a few feet or yards across), whereas in other areas it is coarse (with all the vegetation for dozens of square hectares uniformly burned).

The ability of Yellowstone's large mammals to survive the fires surprised those of us conditioned by Smokey the Bear and Bambi. Contrary to "common knowledge" about the destructiveness of fires, relatively few large mammals died (Singer et al. page 716 this issue). Most large-mammal mortality was the result of smoke inhalation, though many of the carcasses were burned afterward. Large mammals were frequently observed grazing or bedded down in meadows near burning forests; actual flight was rare, and only necessary on days when fires made major runs (Singer et al. page 716 this issue, Singer and Schullery 1989, Mills 1989).

Immediate effects on threatened and endangered animals were light. No peregrine falcons (*Falco peregrinus*), currently the subject of reintroduction work in Yellowstone Park, were known killed by the fires. Five bald eagle (*Haligeetus leucocephalus*) nests were destroyed, but no eagles were known lost (McEneaney 1989). Two grizzly bears are also thought to have perished in the fires.[3]

[3]R. Knight, 1989, personal communication. Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT.

Table 1. Greater Yellowstone areas burned by major fires (in ha).*

Fire	Grand Teton National Park	Yellowstone National Park	Bridger-Teton National Forest	Custer National Forest	Gallatin National Forest	Shoshone National Forest	Targhee National Forest	Total
Clover-Mist		80,310				47,520		127,830
Fan		8360						8360
Hellroaring		7850			18,840			26,690
Huck	1080	10,250	33,150					44,480
Mink Creek		16,620	29,910					46,530
North Fork		196,090			1000		4520	201,610
Snake River		68,810						68,810
Storm Creek		7280		12,280	18,440			38,000
Total	1080	395,570	63,060	12,280	38,280	47,520	4520	562,310

*All figures are preliminary, based on coarse resolution (finest unit of measurement 80 ha) aerial mapping. Figures from GYPFRAC-BAST 1988. A few minor and peripheral fires are not included in totals.

Figure 2. The North Fork Fire moving along the Madison River in Yellowstone National Park in August 1988. Photo: Jeff Henry, National Park Service.

Many small animals died in the fire or attendant smoke (Mills 1989). The fires will result in shifts of relative abundance of various species of birds, mammals, and insects, but there is no evidence to suggest that any individual species will be in danger of extinction because of the fires.[4] Predators took advantage of the loss of cover after the fires to harvest many small mammals. McEneaney (1989) observed more than 40 ferruginous hawks (*Buteo regalis*), a species uncommon in YNP, hunting openly near Hayden Valley, and he proposed that they had followed smoke columns from outside the park to the good hunting grounds.

The fortunes of wildlife in the fires exemplify the complications of public perspectives on the fires. Many observers have spoken reassuringly about the fires as "beneficial" to wildlife, and "good" for the forests and other plant communities. It is true that the fires will in some ways benefit some animals, but there are rhetorical traps in such pronouncements. If the goal of the park is to protect biotic associations and processes rather than promote growth of favored animals, then terms like "good" and "beneficial" are of limited value. The park's ecological processes will, over the course of the next 200–400 years, present various plants and animals with opportunities that will never be the same from year to year. A species advantaged now may be disadvantaged in 40 years. Recent paleoecological research indicates that very nearly the same mammalian fauna

Figure 3. Fire-retardant foam was used on buildings, in this case a residence at Mammoth Hot Springs, 10 September 1988. Most buildings were adequately protected by such techniques. Photo: Jim Peaco, National Park Service.

[4]R. Renkin, 1989, personal communication. Research Division, National Park Service, Yellowstone National Park, WY.

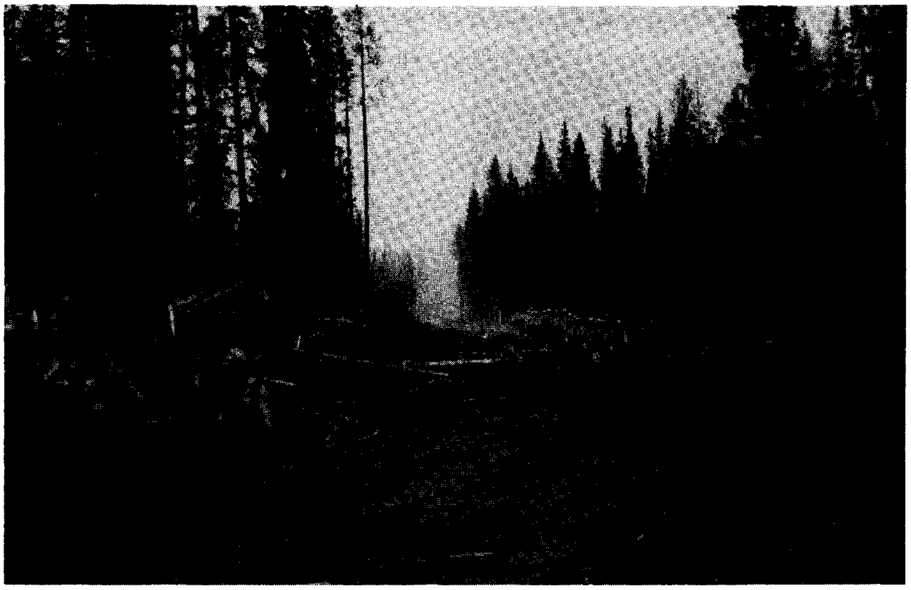


Figure 4. Bulldozers were used to cut fire lines, in this case in Gallatin National Forest near the northeast entrance to Yellowstone National Park and to Cooke City, MT. Fire fighters are moving through a bulldozer-cleared area where all trees have been removed for a width of at least 8 bulldozer blades. Bulldozer lines proved no more effective than hand-dug lines at holding fast-moving fires and left scars that will remain indefinitely. Photo: Jim Peaco, National Park Service.

occurred in Yellowstone 1700 years ago as today,[5] since which time the GYA has probably experienced several major fire events. This continuity of species presence suggests that the 1988 fires should not significantly affect mammalian diversity.

Responses to the fires

The GYA fires may have closely replicated a natural event (Christensen et al. page 678 and Romme and Despain page 695 this issue), but they replicated it in a day when such natural events are extremely inconvenient for society. They were, in many respects, a hardship to the people who live, work, or visit the region, as well as to the local commerce. They were the source of considerable outrage and more than a little tragedy. It has proven difficult for the public to separate the scientific interest and aesthetic wonder of their ecological effects from the consternation of their political and economic effects.

The largest fires were subjected to formal operational reviews by interagency teams, in keeping with established postfire procedures. These evaluations dealt with many aspects of each fire's suppression effort, including bureaucratic procedures, decision making, and actual mechanical implementation of decisions. During the fire season, many controversial decisions were made, and the review process brought out various operational shortcomings. In the long run, the enduring legacy of these review teams may not be in their findings on any specific procedural issue but in the broader view—the fires as a GYA phenomenon, needing improved coordination on an ecosystem-wide level (GYCC 1989).

On 28 September 1988, the secretaries of agriculture and interior created a Fire Management Policy Review Team to evaluate the fire policies of the NPS and the USFS wilderness areas. This interagency team included representatives of the NPS, the USFS, the US Fish and Wildlife Service, the Bureau of Land Management, the Bureau of Indian Affairs, and the National Association of State Foresters. While reaffirming the principles and fundamental importance of allowing fire a role in these public lands, it recommended that fire management plans of various parks and forests must be "strengthened" in some ways aimed at better control of fires (USDA/USDI 1989). Because this process could not be completed in time for the 1989 fire season, Secretary of the Interior Manuel Lujan and Secretary of Agriculture Clayton Yeutter directed their managers to suppress all fires in 1989.

Ecological effects and research opportunities were also examined and projected (Christensen et al. page xxx this issue, Mills 1989, MSU 1988). The scientific community has recognized a unique opportunity to study the effects of ecosystem-wide fires in a relatively pristine setting, but funding problems may cause much of the opportunity to be lost.

The public response will be hardest to measure. Although the principles behind NPS and USFS fire policies were and still may be fairly well received in the specialized scientific and

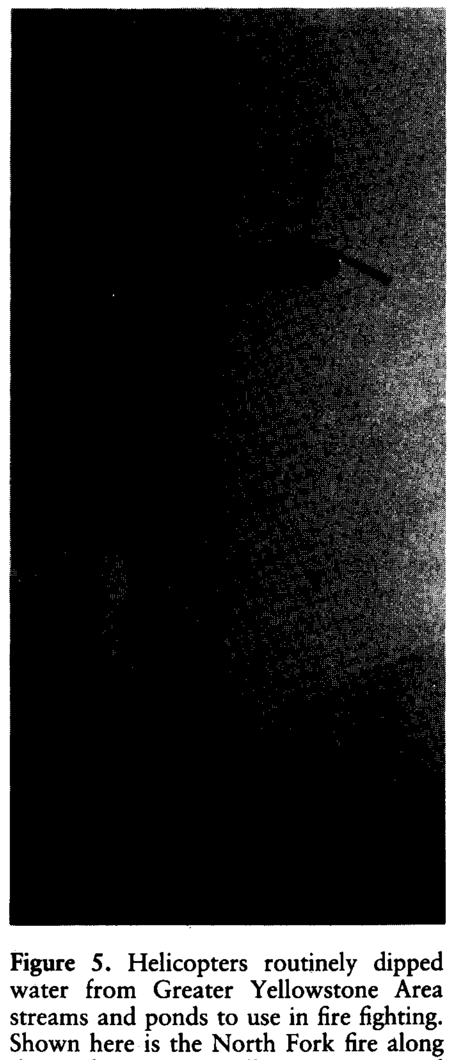


Figure 5. Helicopters routinely dipped water from Greater Yellowstone Area streams and ponds to use in fire fighting. Shown here is the North Fork fire along the Madison River, Yellowstone National Park, August 1988. Photo: Jeff Henry, National Park Service.

[5]E. Hadly, 1989, personal communication. Research Division, National Park Service, Yellowstone National Park, WY.

Mountain ranges are blanketed by smoke from the Mink Creek fire in the Absaroka Mountains, southern Greater Yellowstone Area, 19 August 1988. Photo: Jim Peaco, National Park Service.

conservation communities, they were unknown to the public in the summer of 1988. Even President Reagan professed ignorance of the policies.

Many GYA managers and residents feared that media coverage of the fires gave a sensationalist view of the fires and convinced the public that YNP was destroyed, and analysis of media coverage of the fires has suggested that reporters did misrepresent the situation (Smith 1989a,b). The multiple filters of agency public affairs offices, regional chambers of commerce, and print and electronic media seem in some cases to have stood between the public and an accurate picture of the fires and their ecological significance. The impact of the GYA fires on public consciousness about wildland management and the ecology of fire appears to be considerable, and thereby the 1988 fires may have continued effects on the formulation of public land fire policies for many years.

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Historical Perspective on the Yellowstone Fires of 1988

A reconstruction of prehistoric fire history reveals that comparable fires occurred in the early 1700s

William H. Romme and Don G. Despain

Maintaining an ecosystem shaped primarily by natural geological and ecological processes is a primary goal in Yellowstone National Park (YNP) (Houston 1971). Thus, one important question about the fires of 1988 is whether they were really natural: Did they behave as they would have if Europeans had never entered the area? The park had a policy of complete fire suppression from 1872 to 1972, so past fire control may have led to abnormal fuel conditions and therefore to abnormal fire spread and behavior in 1988 (Dodge 1972, Kilgore and Taylor 1979). In this article, we compare the fires of 1988 with fires during the previous 350 years. We use both information contained in park files and results of our tree-ring research on the prehistoric fire history.

The extensive fires of 1988 should not be viewed as an abnormal event

Fire History

We reconstructed the history of fires in a 129,600-hectare study area located on the subalpine plateaus in south-central YNP (Figure 1). This area, comprising approximately 15% of the park, lies at an elevation of 2400 m and contains dry, infertile habitats on rhyolite substrates as well as more mesic and fertile habitats on andesite and lake-bottom substrates (Despain in press).

From color, low-level aerial photographs we constructed a map of forest patches. We then located in the field each patch that was more than 5 ha, and we collected increment cores (small, nondestructive samples of tree rings from which tree age can be estimated) from 5 to 10 dominant lodgepole pine trees, as well as from cross sections from any fire-scarred trees. Large patches (more than 100 ha) were sampled in at least two areas.

In the lab, we determined the dates of past fires from the fire-scarred sections using dendrochronological methods (Arno and Sneck 1977). Many patches contained no fire-scarred trees; in these patches we determined the date of the last fire from the ages of the dominant lodgepole pine trees.

Finally, we used our map generated from the aerial photographs to determine the areas burned (Arno and Sneck 1977, Heinselman 1973). Because rings are extremely narrow in most fire-scarred trees and fire-scarred trees were not present in many areas, we consider our estimated dates of fires during the last 300 years to be reliable only within one to three years. Therefore, we present the amount of area burned in 10-year intervals.

We also reconstructed the forest mosaics that probably covered our study area at various times during the last 250 years. First we classified the stages of postfire succession after canopy fires on the Yellowstone Plateau by sampling a sequence of stands burned at various times during the last 400 years (Figure 2, bottom). We then drew a map showing the stand age (number of years since the last stand-replacing fire) and successional stage in 1985 of each forest patch. For each patch, we calculated its stand age in 1735 and estimated its successional stage by using the ob-

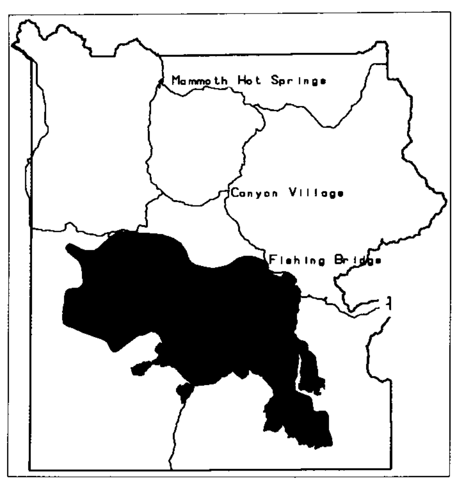

Figure 1. Subalpine study area in south-central Yellowstone National Park.

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served relationship between age and stage. With this approach, we reconstructed mosaics of stand age and probable successional stage for our study area at 20-year intervals from 1735 to 1985. This work was an extension of an earlier study (Romme 1982, Romme and Knight 1982).

The 1988 fires burned more area than was burned in any previous 10-year period within our study area (Figure 2, bottom). The large extent of burn probably was due to weather conditions in 1988; the structure of the forest mosaic in 1988, which was a product of successional events during the last 250–300 years; and the effects of fire suppression in the twentieth century.

The summer of 1988 was the driest since recordkeeping began in YNP in 1886. April and May had been wetter than average, but precipitation in June, July, and August was 20%, 79%, and 10% of normal, respectively (NPS 1988). By late July, the moisture content was as low as 2–3% in dry herbs and dead twigs and 7% in larger dead woody fuels. These dry fuels, combined with high temperatures and extraordinary winds produced by a series of dry high-pressure systems, created some of the most severe burning conditions observed in this century (NPS 1988).[1]

The forest mosaic provided a fuels complex in which fires could burn intensely over large areas under these weather conditions. Our reconstructions indicate that it may have been nearly 300 years since the Yellowstone landscape had been composed of such a flammable mix of forest stands. Figure 2 (top) shows the percent of our study area covered by different forest successional stages (Figure 3) at various times during the last 250 years.

Lodgepole pine (*Pinus contorta*) is the most common tree in YNP, and Despain (in press) has characterized stands there by their age and state of development. Recently burned forests, until the time of canopy closure (approximately 40 years), are classified as LP0. In these forests, large logs do not burn easily and live fuels are usually too green, and small dead fuels too sparse, to carry fire readily. Stands dominated by densely clustered, young, even-aged lodgepole pines are classified as LP1. Fuels on the forest floor are generally sparse, although some large, rotten logs remain from previously fire-killed trees. Crown fires propagate only in extremely windy conditions. This successional stage lasts from approximately 40 to 150 years postfire.

Even-aged closed canopies of lodgepole pines with a developing understory of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are classified as LP2. This stage lasts from approximately 150 to 300 years after a fire. Fuels on the forest floor are sparse to moderate, and flammability begins to increase in the later portions of this stage. Finally, LP3 stands have pine, fir, and spruce of all ages. This stage persists until the next stand-replacing fire. Young spruce, fir, and dead fuels are dense enough to propagate crown fires under dry conditions even without wind.

The earliest successional stages, (LP0, LP1, and the initial period of LP2) which are comparatively less flammable than the older stages (Despain in press, Despain and Sellers 1977), were the most common successional stages in our study area from the mid 1700s through the 1800s. The more flammable older stages have dominated since the early 1900s.

Several extensive fires occurred in our study area between 1690 and 1710 and again between 1730 and 1750 (Figure 2, bottom). Although more recently some fires have occurred in every decade, there were no very large fires, comparable to those of the early 1700s, until 1988. Note that during most of this period there were no Europeans in the region to influence the fire regime. Native Americans had a significant influence on fire frequency in many parts of North America (Barrett 1980, Pyne 1982), but, although their role in high-elevation forests of the Yellowstone region is not well understood, they probably had only a minor influence there. Existing data (Taylor 1964) suggest that Native Americans used the warmer and more productive landscapes at lower elevations more extensively than the high plateaus. Moreover, even if Indians were numerous in our subalpine study area, their major effect on fire history probably was in igniting fires, and ignition sources appear to be far less important than weather and fuel conditions

[1]R. Rothermel, 1989, personal communication. Intermountain Research Station, USDA Forest Service, Missoula, MT.

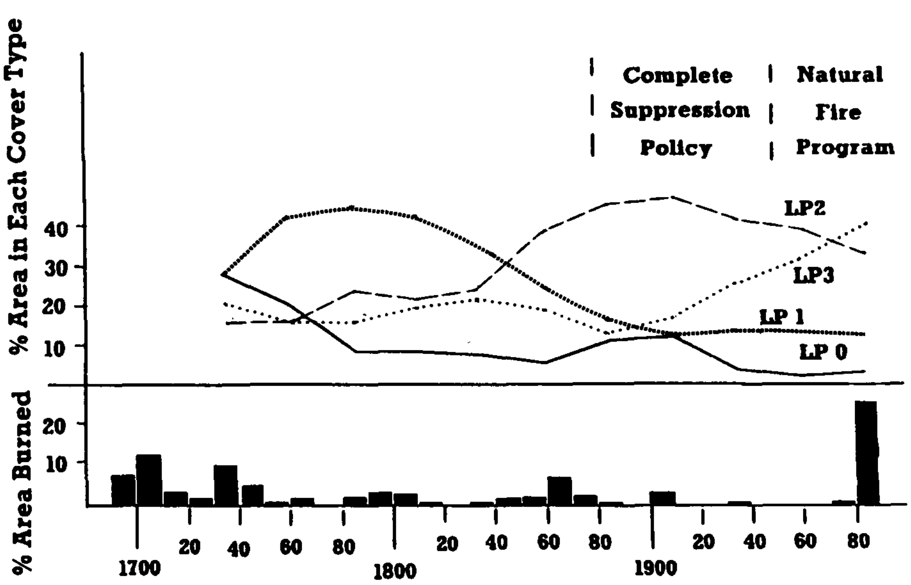

Figure 2. **Top:** Percent of the study area burned by stand-replacing fires in each decade from 1690 to 1988. **Bottom:** Percent of the 129,600-hectare subalpine study area covered by each successional stage from 1735 to 1985. The area covered by meadows, water, and other constant features of the landscape are not included in the figure (Romme 1982). The reconstructions extend back only to 1735 because extensive fires around 1700 destroyed the evidence necessary to reconstruct earlier landscape mosaics.

in determining fire-return interval in this ecosystem.

Why fire activity had been low

We suggest that one important reason for the low level of fire activity during the last 250 years was that the forest mosaic was composed largely of early to middle successional stages, so it had relatively low flammability. Lightning probably ignited fires every summer, but, due to unfavorable fuels complexes, fires were unable to spread over large areas. It is also possible that there simply were no years from 1735 to 1987 with weather conditions as dry and windy as 1988. We cannot tell, because tree rings indicate moisture and temperature conditions, but not wind.

Fires as extensive as those of 1988 probably could have been supported by the vegetation in any year after approximately 1930 (Figure 2, top). We suggest that they did not occur until 1988 because of summer weather conditions and human fire control efforts.

How important was suppression? Park records reveal that lightning ignitions have occurred every summer. Even without suppression, most of these ignitions fail to spread. They occur either in a fuels complex that cannot support fire spread or during a period of wet weather. From 1972 through 1987, 235 lightning-caused fires (an average of 15 per year) were allowed to burn without interference in Yellowstone National Park.[2] All but 15 of these fires (94%) burned less than 40 ha and only 8 (3.4%) were larger than 400 ha. Moreover, only in 5 of these 16 years did the total area burned in the park equal more than 40 ha, and in only 2 years did it exceed 4000 ha.

Organized fire suppression efforts in YNP began in 1886. These early efforts probably were fairly effective along roads and major trails, but they probably had little effect in remote areas on the high plateaus until after World War II, when new fire-fighting methods and technologies became widely available. Written accounts in park records from before the 1940s suggest that often by the time a crew hiked into an inaccessible area, the fire either had gone out or had grown to such a size that it could not be extinguished with the hand tools available.

By the mid-1970s, Yellowstone, Grand Teton National Park, and several of the adjacent National Forest Wilderness Areas had new fire management policies that permitted some lightning-caused fires to burn without interference in backcountry areas (Despain and Sellers 1977). Therefore, the period of consistent fire exclusion in most of Yellowstone National Park, from the mid 1940s until the mid-1970s, spanned approximately 30 years. Even during the

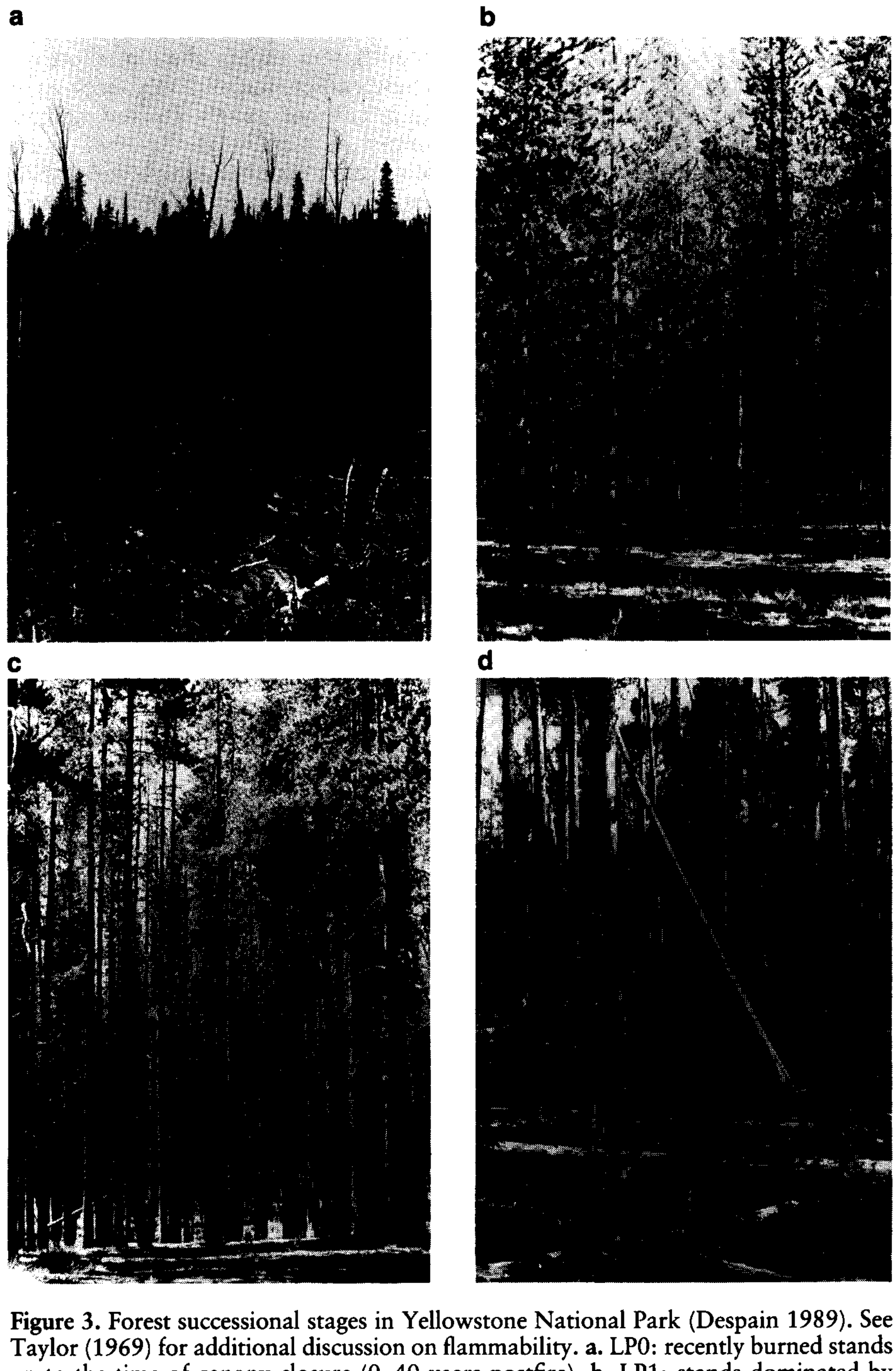

Figure 3. Forest successional stages in Yellowstone National Park (Despain 1989). See Taylor (1969) for additional discussion on flammability. **a.** LP0: recently burned stands up to the time of canopy closure (0–40 years postfire). **b.** LP1: stands dominated by dense, young, even-aged lodgepole pine (*Pinus contorta* var. *latifolia*) (40–150 years postfire). **c.** LP2: even-aged, closed canopy of lodgepole pine stands with a developing understory of lodgepole pine, subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) (150–300 years postfire). **d.** LP3: all-aged stands of pine, fir, and spruce, which persist until the next stand-replacing fire.

[2]Unpublished fire records on file at Yellowstone National Park, WY.

effective suppression period, fires burned hundreds of hectares in some years—1946, 1949, 1953, 1960, 1961, and 1966 (Taylor 1973).

The effect of fire suppression

How then did these 30 or so years of attempted fire exclusion influence fire behavior in 1988? Our data (Figure 2) indicate that the principal effect of fire suppression was to delay the onset of a major fire event, which probably was inevitable given the nature of the fuels complex that had developed since the last extensive fires in the 1700s. Large fires might have burned during the six dry summers from 1946 to 1966 had all lightning-ignited fires not been suppressed. However, these fires probably would not have been as extensive as the fires of 1988 because the weather conditions were less severe. If some of the area that burned in 1988 had burned in those previous years, the 1988 fires might have been smaller.

From this perspective, the fires of the late twentieth century were comparable, in total area burned, to the fires of the late seventeenth and early eighteenth centuries. Stand-replacing fires burned 34% of our study area during the 50-year period from 1690 to 1739, and 26% of our study area during the 49-year period from 1940 to 1988 (Figure 4).

An important difference is that nearly all of the area burned in the most recent half-century was burned in one year rather than being spread out over a few major fire years. What may be the ecological effects? Increased landscape homogeneity could result if a large, single burn was uniform (Turner 1988). However, in many areas, the 1988 burns were quite patchy due to spotting behavior and variation in fuel conditions and topography. This patchiness, combined with differential rates of succession, will maintain a considerable level of heterogeneity in most of our study area.

Were the 1988 fires abnormal?

There are three indications that fire behavior, in terms of heat release, flame height, and rate of spread, was similar in 1988 and in the 1700s. First, we identified even-aged lodgepole pine forests, covering thousands of hectares, that originated after past fires (e.g., in 1703); such stands apparently develop only after severe fires that kill all aboveground biomass and consume much of the organic matter of the forest floor, as occurred in 1988. Second, the differences in fire behavior in 1988 and in uncontrolled lightning-caused fires in 1976, 1979, and 1981 were largely quantitative rather than qualitative. These earlier, uncontrolled fires were as intense or nearly so and spread almost as rapidly as the 1988 fires, but they maintained high intensities and rates of spread for much shorter times. Third, 30 years of fire exclusion does not appear to be long enough to create abnormal fuel conditions in these forests characterized by centuries-long intervals between fires. The accumulations of dead woody fuels observed before the 1988 fires are typical of late successional lodgepole pine stands (Brown 1975). Indeed, early explorers in Yellowstone described dense tangles of dead and fallen trees (e.g., Strong 1875, Langford 1905), long before fire suppression could have produced abnormal changes in fuels.

Although the fuel conditions within any individual stand probably were not abnormal, the extent and continuity of flammable old-growth stands may have been greater in 1988 than they would have been with no previous fire suppression. Because earlier large fires would have created patches of less flammable early successional stages, the more continuous landscape in turn may have allowed the fires in 1988 to burn a larger total area than if fires had burned without interference during the effective suppression period. The actual effectiveness of such hypothetical fire barriers is difficult to assess, however, because in August and September 1988 the fires were jumping over and burning through areas up to 1600 ha that had burned just 10–50 years earlier. Finally, our landscape reconstructions (Figure 2, top) do not show an abrupt change in the landscape mosaic corresponding to the onset of fire suppression; rather they show a continuation of successional dynamics that were initiated almost 300 years earlier.

We conclude, therefore, that the fires of 1988 should not be viewed as an abnormal event. Some of the fires were unnatural in terms of ignition source (three of the eight major fire complexes were caused by people, and these fires were responsible for roughly half of the total area burned). However, numerous lightning ignitions occurred in the vicinity of the human-caused fires in late July and August of 1988. If the human-caused fires had been eliminated and these lightning fires had been allowed to burn without interference, they might have burned a comparable area, although the spatial distribution would have been different.

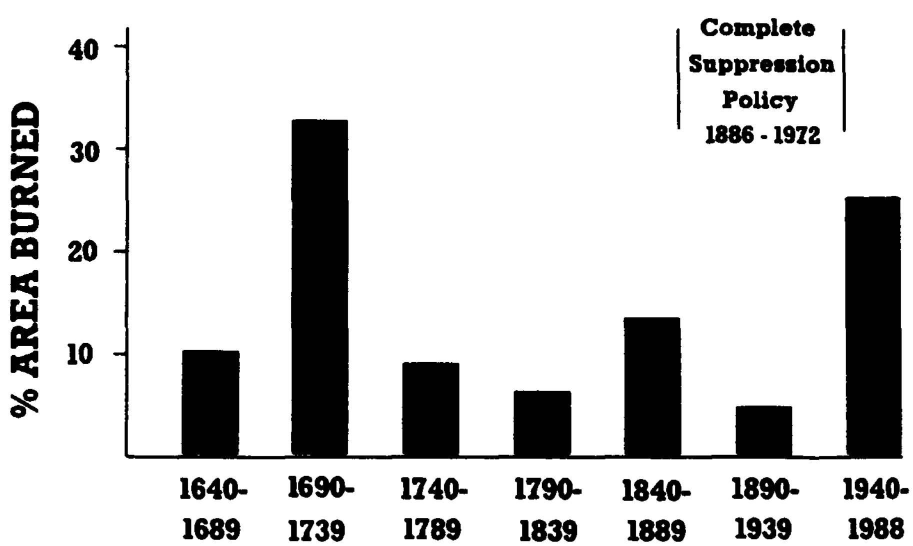

Figure 4. Percent of the area within the study area that burned during each half-century interval from 1640 to 1988.

In terms of total area burned and fire severity, the 1988 fires evidently were similar to those around 1700. Past human actions, mainly fire suppression, had some influence on the size and behavior of the fires in 1988, but these large fires were the result primarily of drought and wind conditions, as well as of normal successional dynamics following the last major fires approximately 280 years ago.

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The Yellowstone Fires: Issues in Landscape Ecology

A landscape perspective is necessary in resolving the difficulties of natural area management

Dennis H. Knight and Linda L. Wallace

Fire policy is only one of many controversies that have characterized the management of Yellowstone National Park (YNP). Some people opposed establishment of the park in the first place, fearing that it would detract from economic development. Later there were arguments about whether or not predator control was necessary to increase the abundance of big game. Currently the reintroduction of wolves (*Canis lupus*) is being debated, and there is considerable pressure to reduce the elk (*Cervus elaphus*) population. Another controversy developed over whether the Greater Yellowstone Area (GYA) is large enough to support grizzly bears (*Ursus arctos*) without supplemental food. Park management policies continue to evolve as new information is obtained.

The effects of fire suppression, predator control, and supplemental feeding often have been difficult to assess. To be sure, they have changed the character of Yellowstone. As Aldo Leopold wrote about Glacier National Park in 1927, "The balance of nature in any strict sense has been upset long ago . . . The only option we have is to create a new balance objectively determined for each area in accordance with the intended use of that area."[1]

New opportunities exist in Yellowstone to understand effects of disturbances

But how can the intended use of a wilderness area be objectively determined? Is it a matter to be decided by public opinion? What can science contribute? In this article, we take a landscape perspective in synthesizing ecological information and concepts relevant to the continuing challenge of natural area management. We address fire-caused temporal and spatial variability in vegetation patterns, plant-animal relationships, and land-water interactions in YNP.

Temporal and spatial scales in Yellowstone

All landscape mosaics change through time, and it is unrealistic to expect that Yellowstone should not change as well. On a scale of millennia, it has changed since the retreat of the glaciers, and, on a scale of centuries, it has changed since the large fires of the early 1700s (Romme and Despain page 695 this issue). Shifts in climatic conditions have caused landscape changes at both time scales, as have such disturbances as fires and insect outbreaks.

Some would argue that national parks are too small, or too strongly affected by humans, to allow disturbances such as fire to occur uncontolled (Bonnicksen 1988, 1989). Although true for many natural areas, Yellowstone is one of the largest US parks. If it is too small, the 1988 fires—the most significant disturbance event in YNP in over a century—probably will cause the demise of certain park features that managers, scientists, and the general public feel are important. Asserting with confidence that YNP is large enough for uncontrolled disturbances is not possible with available information, but after the fires, extensive tracts of unburned forest remain and wildlife is expected to recover (Christensen et al. page 678 this issue).

The pre-1988 Yellowstone landscape consisted of a mosaic of meadows, aquatic ecosystems, unforested ridges and peaks, geyser basins with little vegetation, and forests of different species composition and age (i.e., successional stages since previous disturbances). This spatial mosaic is a function of past disturbances superimposed on environmental gradients, whether abrupt or gradual. The fires of 1988 burned unevenly across this sometimes patchy, sometimes homogeneous landscape. In some areas, the patchiness was increased by the fires; in others the fires appear to have caused more uniformity. In either case, research is necessary to determine if the area and spatial variability of the park are sufficient to maintain

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[1]Letter from Aldo Leopold to Charles J. Kraebel, Superintendent of Glacier National Park, 18 January 1927.

the processes, biotic diversity, and other features that make Yellowstone unique.

Temporal and spatial patterns in terrestrial vegetation

In general, the terrestrial vegetation of the Yellowstone region is characterized by extensive lodgepole pine (*Pinus contorta* var. *latifolia*) forests, sporadic forests of Engelmann spruce (*Picea engelmanii*) and subalpine fir (*Abies lasiocarpa*) at higher elevations, Douglas fir (*Pseudotsugu menziesii*) forests and woodlands at lower elevations, scattered aspen (*Populus tremuloides*) groves, woodlands dominated by limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*), occasional sagebrush (*Artemisia tridentata*) grasslands and mountain meadows, and riparian vegetation comprised of sedge/grass meadows and willow (*Salix* spp.) thickets (Despain 1973, Romme and Knight 1982). Fire has played an important role in shaping vegetation distribution patterns (Despain and Sellers 1977, Gruell and Loop 1974, Houston 1973, Loope and Gruell 1973, Romme 1982, Romme and Despain page 695 this issue, Romme and Knight 1982, Taylor 1969, 1973, 1974). Sharp transitions from young to old forest are readily apparent, marking the boundaries of earlier fires. Fire-scarred trees are common, and charcoal is easy to find in the surface soil of forested areas.

Plant adaptations. The plants are well adapted to fire. The serotinous (closed cone) feature of lodgepole pine is mentioned often in this regard, and it is interpreted as an adaptation for taking advantage of the abundant water, nutrients, and space made available for new plants immediately after a burn (Lotan 1975, Muir and Lotan 1985a,b). Such cones allow for the storage of large quantities of seed during periods of many years, with the seed being dispersed when the heat of a fire cracks the resin bonds on cone scales. Apparently few of the seeds are burned. Cone serotiny allows for the development of the even-aged stands (±20 years or more) that characterize much of the Rocky Mountains where fire is a frequent disturbance.

Interestingly, not all lodgepole pine are serotinous. Muir and Lotan (1985a) found that serotinous and nonserotinous trees usually coexist, with the relative abundance of each dependent on the last disturbance. They observed that where the last major disturbance was caused by factors other than fire (e.g., insects or wind), more of the lodgepole pine are nonserotinous. With the long time period between fires in most subalpine coniferous forests in the GYA, especially where fire suppression was effective, there is a greater chance for nonserotinous trees to be more common. The proportion of each reproductive strategy before 1988 is unknown, but it probably varied considerably from place to place.

The serotinous cones of lodgepole pines are unique, but other plants are adapted to fire as well. Most of the grasses, forbs, and shrubs are capable of sprouting, an adaptation that surely must have evolved as a means of surviving fire as well as grazing, drought, and cold winters. Aboveground parts of many plants may be charred or even completely burned, but much of the root system remains unharmed because soil temperatures commonly are not elevated to lethal limits. Energy reserves in the surviving root systems allow for the production of new stems and leaves within a year, and the increased availability of sunlight, water, and nutrients allows for increased seed production, which facilitates the establishment of new plants.

Predicting regrowth. In the Yellowstone area, ecosystem development after fire is easiest to predict where sprouting growth forms were dominant before the fires. For example, burned aspen groves are expected to respond quickly by root sprouting (Jones and DeByle 1985). Most of the understory plants will sprout also. Although the physiognomy of the groves will be altered dramatically, with a high density of young sprouts instead of widely spaced older trees, the species composition changes comparatively little, and the aspen grow rapidly.

Much the same scenario is appropriate for the riparian meadows and shrublands. Here, too, most of the plants are expected to resprout vigorously, and the changes will be mainly physiognomic (Leege 1969). Browsing by herbivores may increase because of the increased abundance of more succulent and possibly more nutritious sprouts. As with the aspen groves, scientists have the opportunity to observe recovery in the presence of large ungulate populations and to ascertain how well the plants

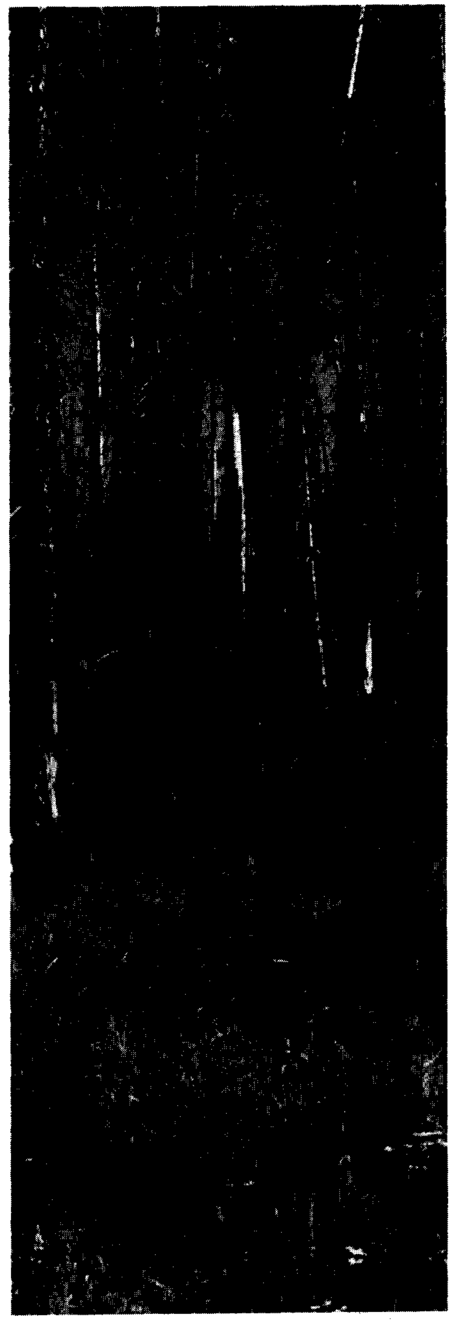

Figure 1. Burned forest two years after a 1979 fire in Yellowstone National Park, showing high understory cover and many standing dead trees. Some areas of this burn have less understory cover than shown in this photo.

are adapted to high levels of herbivory.

Grasslands with big sagebrush are common in some parts of the GYA and probably were altered more dramatically than the riparian vegetation and aspen groves. Big sagebrush, often the dominant plant, cannot sprout, and thus it is greatly reduced in abundance after fires. However, surviving sagebrush plants produce many seeds, which germinate readily. Sprouting grasses and forbs are the dominants until new sagebrush seedlings become established and grow to maturity, perhaps 15 to 30 years later. Big sagebrush can be an important winter food, especially for mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocarpa americana*). The impact of this food loss remains to be seen, but only a small portion (9%) of YNP's winter range was burned.

During the next few decades, the effects of the fires are expected to be most easily seen in the coniferous forests, as none of the conifers in Yellowstone have the ability to sprout. Where aspen coexisted with conifers, the forest will likely be converted temporarily to aspen. However, the spruce, fir, and pines are expected to become dominant again in most areas after a century or more (Stahelin 1943, Peet 1988).

Forest regeneration is expected to be slower where aspen was absent. Initially, the grasses, sedges, forbs, and shrubs may form a dense cover under the standing trees killed by the fire (Figure 1). Species composition is expected to vary greatly, as is the amount of cover, and typically the herbaceous plants appear unusually green and lush—an indication of improved water and nutrient availability. In some areas, the growth of herbs and shrubs is expected to be slow because the fire was unusually hot, killing root systems and organisms important for plant growth (e.g., mycorrhizal fungi), because tree density before the fires was high enough to preclude understory plants, or because of severe environmental conditions.

Tree seedlings are expected to become obvious 5–10 years after the fires and could be dense where serotinous lodgepole pine dominated the forest. Where the pines were not serotinous, or where spruce and subalpine fir were the dominants, tree seedlings and saplings may be sparse for one or more decades. Some areas could become meadows if conditions are marginal for tree growth, whether due to intense competition from herbaceous vegetation or environmental conditions that prevent tree seedling establishment (Stahelin 1943).

Although the prospect of forest-to-meadow conversions may be alarming to some, this conversion probably has occurred before. Meadows can enhance wildlife habitat and landscape diversity.

However, conifers are likely to become re-established in most of the burned coniferous forests. Lodgepole pine or Engelmann spruce probably will be the most common dominants in the young forest, with Douglas fir well represented at lower elevations. These three species seem best adapted for seedling establishment on mineral soil in open areas (Alexander 1987). Lodgepole pine (and some aspen) seedlings were commonly observed in intensively burned forest in 1989.

Standing dead trees from the 1988 fires are expected to be conspicuous for 20 years or more, but some will fall each year until the snags are a minor feature of the landscape. The successional sequences can vary considerably (Aplet et al. 1988, Brown 1975, Despain 1983, Romme and Knight 1981, Stahelin 1943, Veblen 1986, Whipple and Dix 1979), a fact that contributed to the vegetation diversity that existed in Yellowstone before the 1988 fires and which is expected to prevail again as the mosaic of successional patterns becomes superimposed on the burn mosaic. Of course, the forests that were not burned in 1988 will continue to change as well.

Research opportunities. YNP now provides unique opportunities for research on postfire succession because the fires created so many variations in factors that influence community change (topographic position, soil characteristics, burn intensity, preburn species composition, preburn tree density, seed bank species composition, distance from unburned forest, intensity of postfire herbivory, patchiness of the burn mosaic, and climatic conditions in the first few years after the fires). Such a wide range of conditions rarely occurs in wildlands that have been managed to a large extent for their educational and scientific value. Also, YNP provides opportunities for long-term research. The results should be applicable to resource interpretation and management in the park and throughout the region.

Another opportunity for study is the invasion by introduced plants. There might appear to be little basis for concern about damage by introduced plants, because weed populations in the park were low before the fires, with most species restricted to road ditches and other areas of human impact. Previous fires apparently had not provided habitat for such plants. However, the last large fires occurred around 1700, when there were no seed sources for exotic plants adjacent to the park. Now such plants are abundant nearby. Furthermore, the extensive fires of 1988 created invasion corridors into the park (i.e., open habitats where nonsprouting conifers were killed by fire and where fire-fighting activities scarified the soil).

A third research opportunity pertains to the effects of fire suppression. Despite confident pronouncements about fire suppression causing the large-scale 1988 fires, such effects undoubtedly varied from place to place. Houston (1982) showed clearly that fire suppression led to an increase in the density of Douglas fir and sagebrush at lower elevations in the north, but other information suggests that fuel accumulation is slow on the higher Yellowstone Plateau—so slow that 40 years of effective fire suppression (since the mid-1940s) would have had a minor effect (Romme and Despain page 695 this issue). During the drought of 1988, young forests with little fuel burned along with the highly flammable old growth.[2]

An interesting dimension to the fire suppression issue is the importance of Indian fires before Europeans arrived. Some suggest that such fires kept the forests of Yellowstone more open and less flammable, especially the northern Douglas fir forests at lower eleva-

[2]Richard Rothermel, 1989, personal communication. Intermountain Research Station, USDA Forest Service, Missoula, MT.

tions (Barrett and Arno 1982). Elsewhere, however, the journals of early explorers in Yellowstone suggest dense forests. For example, General W. E. Strong wrote after his 1875 trip into Yellowstone (Strong 1968), "The trees have been falling here for centuries, and such a network of limbs, trunks, and stumps has been formed, that to face it with a horse . . . is enough to appall the stoutest heart . . . The woods are fearful to travel through, covered with . . . pine . . . so thick and close that our horses could, at times, barely squeeze through. . . ."

Shifting animal distribution patterns

Approximately 25–30% of YNP (and a smaller percentage of the GYA) was affected in 1988 by canopy fires, which greatly modified forest physiognomy. Abundant dead and dying trees now stand in these areas, creating habitat very different from the unburned forest. Herbaceous or shrubby vegetation accounts for most of the photosynthesis in areas subjected to canopy fires; berries and other fleshy fruits will become more common. The habitat is more open, and an edge (between burned and unburned forest) favorable for some wildlife has been created in some areas. Prey animals such as small rodents are more visible and, not surprisingly, raptors and some insectivorous birds are attracted to the burned forests (Taylor and Barmore 1980). In general, within a few years after fires, species diversity of plants and animals is higher (Taylor 1973, Taylor and Barmore 1980).

Edges. Aerial views of the Yellowstone landscape suggest that more edge has been created by some fires than others (see page 682). However, data must be collected to verify this observation, as some fires burned across edges between young and old forest during the unusual drought conditions of 1988. Observations thus far suggest that the early summer burns were more patchy, thereby creating more edge, whereas burning later in the summer was more uniform and more likely to cross edges when fuels were drier and winds stronger.

The edges created by the fires are not just a matter of physiognomic discontinuities, with food and cover in close proximity. Burned patches usually are fringed by a halo of trees with brown needles, the result of singeing where fire intensity was inadequate for complete combustion. Some of these trees die because the proportion of singed needles is too high or because too much of the cambium of the thin-barked lodgepole pine has been burned. However, others survive. Fire-scarred trees dating back to 1988 are expected to delineate the fire mosaic long after it is no longer conspicuous.

Furthermore, trees scarred by fire could serve as epicenters for outbreaks of insects such as mountain pine beetles (*Dendroetonus ponderosae*; Gara et al. 1985, Geiszler et al. 1980). Insect outbreaks could contribute to the development of a fuel complex that makes fires more probable in future drought years (Knight 1987). In this way, disturbances of one kind have an influence on the spread of disturbances of other kinds—a primary theme in landscape ecology (Turner 1987).

Insect outbreaks in the singed-tree halos may, however, be kept in check by insectivorous birds. Woodpeckers are known to be more common in burned areas (Taylor and Barmore 1980), and they undoubtedly will feed among the weakened trees on the edge as well, where some insects could be more common. The edge created by a burn is more complex than the edge created by timber harvesting, and the great diversity of complex edges created in Yellowstone provides excellent opportunities for research on predator-prey relationships.

Ungulates. The population sizes and foraging areas of large mammals also are expected to be affected by the fire-caused changes in vegetation (Singer et al. page 716 this issue). These changes could have significant effects on nutrient transfer and the productivity of different parts of the mosaic. In general, some ungulates use the forest edge, commonly selecting habitats with forage and cover in close proximity. New edges could be more attractive than old edges because of the vigorous growth of herbaceous plants that typically occurs after fires. Nutrient availability for the plants in such sites is enhanced by reduced competition from trees, but also because of nutrient accumulation through urine and feces. Also, herbivory is known to affect the rate and direction of nutrient movement (Merrill 1978, Ruess and McNaughton 1988, Schimel et al. 1986). Furthermore, the postfire forage often is more nutritious (McNaughton 1979, Wood 1988) and the ratio of green tissue to dead or supportive tissue is higher than elsewhere, two factors contributing to foraging efficiency.

After fires, ungulates can establish new movement corridors linking water, bedding grounds, calving areas, and summer and winter ranges. Animals can influence rates of productivity and vegetation development, and thereby they could affect the landscape mosaic that develops. Yellowstone now provides excellent opportunities for studies on the interaction of fire, free-roaming ungulates, and vegetation recovery across a variable landscape that is comparatively free from logging activity and roads.

Land-water-nutrient interactions

Disturbances to terrestrial ecosystems invariably lead to changes in aquatic ecosystems (Minshall et al. page 707 this issue). Leaf-area reduction in coniferous forests, whether due to fire or insects, reduces evapotranspiration and increases subsequent streamflow. With reduced canopy cover and nutrient uptake after fires, there is increased potential for erosion and nutrient losses from the upland (Knight et al. 1985). In addition to flooding, there is the potential for declines in soil fertility that affect subsequent successional patterns and increases in sedimentation and nutrient inputs that affect stream and lake productivity. Predicting the outcome in Yellowstone is still a challenge.

Flooding. Flooding that could have adverse effects on downstream settlements is a distinct possibility. However, it did not occur in 1989, even though snowpack water equivalents were average or slightly above (99–120% of a 30-year average), because climactic conditions were conducive

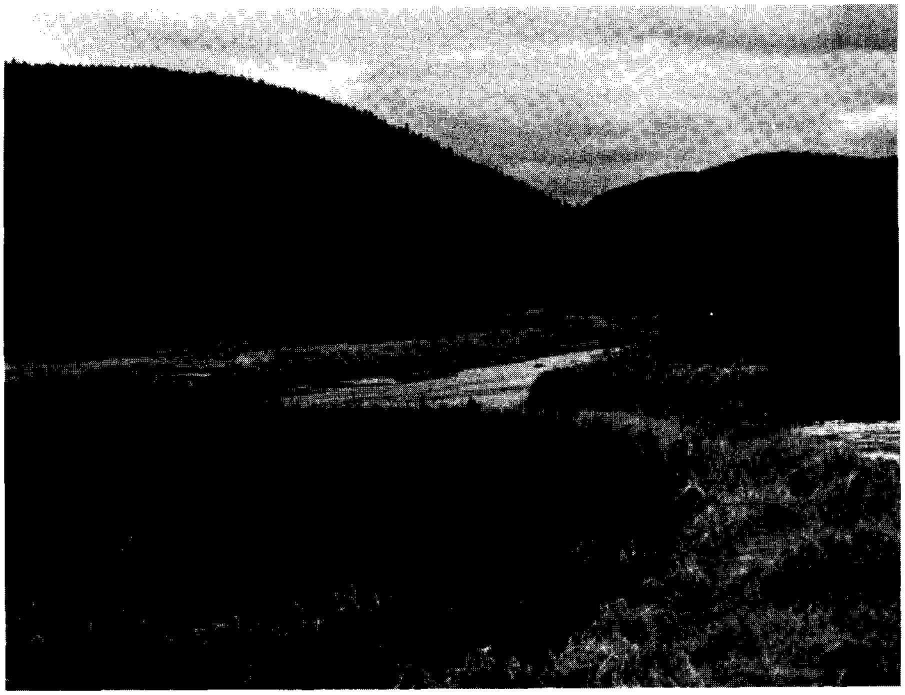

Figure 2. A broad riparian zone typical of some rivers in the Yellowstone area. Elsewhere the riparian zone may be more narrow, providing little filtering capacity for sediments and nutrients originating on the upland.

to slow snowmelt.[3] Also, the lack of dramatically increased streamflow in 1989 can be partially attributed to high soil storage capacity due to the 1988 drought. With reduced evapotranspiration in 1989 due to less leaf area in burned areas, the soil is expected to have less storage capacity in 1990 and the potential for flooding could be considerably higher. After lumber operations, increased streamflow has been observed in some areas for 25 years or more—the time required for the restoration of the original amounts of leaf area and canopy cover (Troendle 1983).

Concerned about the potential for flooding, the Soil Conservation Service used a regression model for predicting the effects of fires on streamflow in the GYA (Farnes and Hartman 1989). Their model incorporated data on reduced forest cover due to canopy fires. Assuming typical climatic conditions, spring streamflow was predicted to increase by no more than 2–13%, depending on watershed characteristics. Increases of this magnitude should not create flooding problems for downstream settlements, unless precipitation is abnormally high. In fact, the additional streamflow could be a welcome addition to currently low water levels in downstream reservoirs.

[3]P. E. Farnes, 1989, personal communication. Soil Conservation Service, Bozeman, MT.

Erosion. Although erosion can degrade soil fertility or water quality, the occasional episodes of erosion in the GYA probably are tolerable because background levels are so low. Some bottom sediments from lakes have layers with charcoal fragments, suggesting that erosion after fires has occurred in the past (Mehringer 1985). In 1989, rivers were sometimes black with sediments after heavy rains.

Yellowstone streams and rivers are often fringed by riparian meadows and shrublands that filter sediments during some periods of erosion (Figure 2), thereby minimizing the amount of sediments entering the water. In other areas, however, surface runoff from adjacent uplands could be channelized before it reaches the riparian zone, with the result that little riparian filtration is possible and the sediment load is added to the stream. Observations in 1989 indicate that erosion after rainstorms was greater than during snowmelt.

The riparian zones, as elsewhere, experienced different intensities of burning. In the most severely burned areas, sedge peat was burned down to mineral soil, killing the rhizomes and root systems. In other riparian areas, sprouting is vigorous. The rapid regrowth and accompanying nutrient uptake of lightly burned areas could actually increase filtering capacity, whereas the severely burned areas will have reduced filtering capacities. The fires provide exceptional opportunities for research on the effects of disturbances at the terrestrial-aquatic interface.

Nutrient losses. Even without erosion, there is the potential for nutrient losses from the burned forest soils, with the loss of limiting elements such as nitrogen being of special interest. Some nitrogen is volatilized during fires, but this loss probably is minor compared to losses via leaching as water percolates down through the soil profile. Nitrification typically accelerates after disturbances in coniferous forests, converting the relatively immobile ammonium cation to the highly leachable nitrate (Fisher and Gosz 1986, Hart et al. 1981, Vitousek and Mellilo 1979). As a result, the nitrogen pool in the soil may decline for a period of time (Fahey et al. 1985, Fahey and Knight 1986). However, the loss of nitrogen after fire probably is not a problem, because the nitrogen requirements of the early postfire vegetation are small and the nitrogen lost by volatilization and leaching is replaced by continued atmospheric deposition, fixation, and decomposition of soil organic matter (the largest pool of nitrogen in the forest ecosystem; Fahey et al. 1985).

A portion of postfire nutrient losses from upland areas becomes a gain of nutrients for aquatic ecosystems. Limnologists are now challenged with determining if and for how long stream and lake productivity increase as a result of the 1988 fires (Minshall et al. page 707 this issue).

Variation. From a landscape perspective, the effects of fires on water quantity and quality will vary greatly from one watershed to another. Streams draining watersheds that have been completely burned and that have a narrow riparian zone (low filtering capacity) will be affected more dramatically, with the effect diminishing as the size of the riparian zone increases or as the extent of burning decreases. A promising parameter to compare with various water-quality characteristics is the ratio between the proportion of the upland that was burned to the proportion of the watershed that is riparian (burned or unburned; Figure 3). Such ratios could be usefully integrated with information on burn intensity, the degree of burn patchiness, and slope steepness.

Determining the quantitative relationships between landscape variables, water quality, and stream or lake productivity has been proposed by others (e.g., Lee and Gosselink 1988) and seems especially feasible in Yellowstone, again because such a wide range of conditions could be examined. Rather than the traditional comparisons of burned and unburned watersheds, a gradient analysis of burn effects is possible. A significant advantage of conducting such studies in YNP is that the effects of roads and other human influences would be minimized.

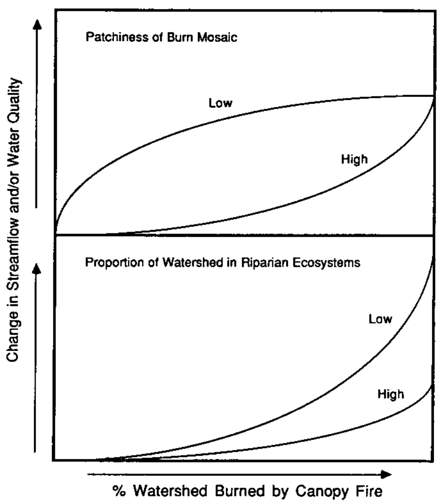

Figure 3. Hypothetical relationships between changes in streamflow or water quality, percent of watershed burned, patchiness of the burned landscape (top), and the proportion of the burned watershed in riparian ecosystems (burned or unburned) that could filter nutrients and sediments (bottom).

Conclusions

In general, the effects of the 1988 fires on terrestrial vegetation are expected to be more vigorous herbaceous vegetation for several decades; a larger portion of YNP in young forests or nonforested area; aspen forests over a larger area, though still a small portion of the park; less sagebrush in some areas for a decade or more; and a larger area of open woodlands or savannas, especially at lower elevations where mature, thick-barked Douglas fir predominated and the fires were less intense. Concomitant changes can be expected in animal population sizes, animal distribution, and some predator-prey relationships. Sediment and nutrient additions to aquatic ecosystems will vary with the extent, patchiness, and intensity of fires and with the filtering capacity of the riparian zone.

Research suggests that most plants are well adapted to fire and that biotic diversity in the GYA will not decline as a result of the 1988 fires. Change continues in ways that influence natural selection. Like acid precipitation, atmospheric carbon dioxide enrichment, the spread of toxins, and various issues in wildlife management, the Yellowstone fires have challenged ecologists to extend their data and research to the scale of landscapes and the biosphere. In all cases, there are many uncertainties due to the complexity of the interactions and the diverse mosaic. Learning the far-reaching effects of changing (or static) landscape mosaics is perhaps the greatest challenge.

The 1988 fires stimulated new interest in the management of natural areas. The inevitability and importance of disturbances are widely recognized (Loucks 1970, Pickett and White 1985, Wright 1974), but some scientists and politicians alike had not thought enough about the historical evidence suggesting that truly large fires occur at intervals of two or more centuries. Others thought that generalizations were possible over large areas such as YNP, or that somehow the park would never (or should never) change in any significant way. The debates that developed, though often ill-conceived from a scientific viewpoint, stimulated great public interest and highlighted the difficulties of natural area management.

Aldo Leopold called for objectively determined goals in natural area management. If such goals are possible, they must reflect the results of past research. They also must be flexible, as there is much that is not known about the ecological phenomena that we seek to protect.

Additional opportunities now exist in Yellowstone to better understand the effects of disturbances on interactions within and between the patches of specific community types that comprise the landscape mosaic and how changes in the mosaic affect animal populations, aquatic ecosystems, and the spread of future disturbances. Because of its large size, the park now more than ever can provide a basis for refining land management policies in the GYA and beyond. An unusually large segment of the public will be interested in the results.

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Wildfires and Yellowstone's Stream Ecosystems

A temporal perspective shows that aquatic recovery parallels forest succession

G. Wayne Minshall, James T. Brock, and John D. Varley

Few studies have examined the effect of fire on the aquatic biota, and none has adequately addressed major aspects of aquatic ecosystem function. Most of the research has examined the effects of fire on water chemistry (Schindler et al. 1980, Tiedemann et al. 1979). Nevertheless, it is possible to develop a set of predictions regarding the immediate, near-term, and long-term consequences of the 1988 fires in the Greater Yellowstone Area (GYA) by supplementing the existing information base on fire response and general ecological behavior of aquatic ecosystems with knowledge of the response of aquatic systems to logging and to physical disturbances within the channel.

Of the 0.57 million ha of the GYA that burned (Burned Area Survey Team 1988), most (95%) of the area was forest, and the remainder was meadow, grassland, and sagebrush scrubland. Twenty separate river basins or major subbasins were affected by the fires to various degrees (Figure 1). Within Yellowstone National Park (YNP), approximately 32% (1380 km^2) of the stream system was influenced by the fires. In addition, the four large oligotrophic lakes (Yellowstone, Shoshone, Lewis, and Heart lakes), which together make up 94% of the park's water area, had significant portions of their drainages burned (Figure 1). Twenty-eight percent of the Yellowstone Lake watershed, 8% of the Shoshone Lake drainage, 33% of the Lewis Lake drainage, and 50% of the Heart Lake watershed were affected by fire to some degree.

Effects of the fires are likely to be most pronounced in headwaters

In general, loss of vegetation is expected to increase water runoff, but not beyond the normal variability of the hydrologic systems. Due to differences in landscape morphology and in the nature of the fires, streams in the Madison, Upper Yellowstone (above Yellowstone Lake), and Snake river drainages are less likely to be affected by the 1988 fires than the other main river systems in the GYA.

The major effects are expected to parallel the forest recovery and, during the next 300 years, gradually return the aquatic ecosystem to the prefire state. The fires are expected to alter buildup of woody debris, sediment suspension, nutrient cycling, leaf litter input, and the types of aquatic organisms present. These effects are expected to be more pronounced in headwater streams, and they are likely to diminish with increased stream size.

Fire and landscape heterogeneity

The heterogeneous nature of the landscape, due in part to the varying extents of patchiness of the 1988 fires (Figure 1), has important implications for the fire impact on GYA stream ecosystems. The intensity of each fire varied from hot canopy fires (61% of the burned area), to cooler ground fires, to unburned patches of less than 50 ha. Although the percentage of each burn type was remarkably similar among the six major fires, the extent of patchiness varied considerably. Fires early in the summer, when fuel-moisture levels were higher, generally were patchier than those that burned later. After July 21, fires frequently were driven by 65–95 km/hr winds and tended to include wide swathes of continuous canopy burn with spotting by secondary fires to the sides and in front.

Fire impact on different streams is expected to vary proportionally with the intensity and extent of burning of a watershed and the vegetation formerly present. Responses are most likely to be seen in watersheds where the upper portions were heavily forested and were extensively burned (e.g., Lava, Tower, and Blacktail Deer creeks).

The impact also is expected to vary along a given stream system. The greatest impacts of fire probably will be seen in smaller (headwater) streams, and the effects will progressively dissipate downstream, except in reaches where fire-perturbed small tributaries enter a large mainstem

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The Shoshone fire, later reclassified as part of the Snake River complex, seen from Yellowstone Lake shore in late August. Photo: Jeff Henry, National Park Service.

river. The watersheds with small streams (first and second order)[1] commonly burned entirely, whereas watersheds with larger streams (fourth order or larger) rarely did so. Cache Creek and Hellroaring Creek are the only watersheds in which the portions greater than third order received substantial burning. Most of the GYA streams that support a major sport fishery (Firehole, Gallatin, Gardner, Gibbon, Lower Lamar, Madison, and Yellowstone rivers) are larger than fourth order, and thus they were affected little by the fires in their lower reaches.

The impact of the fire in each drainage also is regulated by factors affecting runoff and erosion. These factors include the physical make-up of the area (slope, aspect, elevation, gradient, geology, and soil depth) and climatic variables (temperature, precipitation, insolation, and storm intensity and frequency; Hydrology Assessment Team 1988, Minshall and Brock in press). Increases in flood potential and sediment yield are greatest in the upper subdrainages of Lamar River, Crandall Creek, and North Fork Shoshone River. These subdrainages are characterized by steep slopes (greater than 45%), shallow soils, unstable geology, and intense summer thunderstorms (Hydrology Assessment Team 1988).

In the Madison, upper Yellowstone, and Snake river systems, slopes generally are less steep, valley bottoms wider, and stream gradients lower. Also, the proportion of burned area on steep slopes is smaller. The result is that, even with some increases in water yield due to the reduction of vegetation by fire, the time of concentration of streamflow is lengthened by basin morphology, flood peaks are better regulated, and flooding is less likely (Hydrology Assessment Team 1988).

Temporal responses of stream ecosystems to fire

Stream ecosystem responses are closely linked to terrestrial plant conditions in the surrounding watershed (Hynes 1975, Minshall et al. 1985, Vannote et al. 1980). Therefore, changes in the structure and composition of terrestrial vegetation after wildfire (Arno et al. 1985, Lyon 1984, Romme 1982) may be expected to influence the adjacent streams. Because forest regeneration after wildfire is a long-term process, with a cycle of approximately 300 years, stream ecosystems are likely to respond similarly and shift in concert with temporal changes in plant community structure.

Current understanding of stream ecosystem dynamics provides a rich base from which to postulate specific changes in stream ecosystems as a result of forest changes after wildfire. Paramount to such understanding is the recognition of the crucial link between the food available and the feeding characteristics of the fauna in streams (Cummins 1974, Molles 1982). It is also important to recognize the influence of stream size as a modifier of land-water interactions (Minshall et al. 1985, Vannote et al. 1980).

The effects of fire on aquatic ecosystems can be partitioned into immediate effects that arise directly from the fire (e.g., increased temperature,

[1]In stream terminology, the smallest unbranched tributaries are *first order*. Two first-order streams join to form a second-order stream. The world's largest rivers (e.g., Amazon or Mississippi) are tenth to twelth order.

altered water chemistry, and abrupt change in food quality) and delayed impacts. Some of these delayed effects are primarily physical disturbances associated with increased runoff. These effects are likely to exert their maximal impact within the first one to four years after a fire. In addition, there are likely to be longer-term alterations associated with the removal and eventual successional replacement of the riparian and terrestrial vegetative cover (Figure 2) and consequent alteration of food resources and retention capacity in the stream (Likens and Bilby 1982, Molles 1982).

Immediate effects. Except in small water bodies (first-order streams and small seeps), the high specific heat of water and replenishment from cool groundwater sources are likely to have prevented the heat from the Yellowstone fires from seriously damaging the aquatic biota. Cushing and Olson (1963) recorded a 10° C increase in temperature for a short time in a small, slow-moving stream after the burning of weeds that covered the stream and its banks. Trout (*Oncorhynchus mykiss,* formerly *Salmo gairdneri*) in wire-mesh cages showed marked distress but did not die. Heat fracturing of the surfaces of rocks in first-order streams and incineration or scorching of exposed and shallowly submerged aquatic plants have been observed in GYA.[2] However, in most cases the fires are thought to have heated the water at most a few degrees (Albin 1979, Ice 1980). In larger streams, such as the Firehole River, shading by dense clouds of smoke actually may have reduced water temperatures compared to those on a clear day (Ice 1980).[3]

Data from previous fire experience indicate that few, if any, adverse effects of the Yellowstone fires on water chemistry are to be expected (Johnson and Needham 1966, Schindler et al. 1980, Tiedemann et al. 1978, Wright 1976). Instead, algal growth may be temporarily stimulated to levels considered beneficial (Albin 1979, McColl and Grigal 1975). However,

[2]G. W. Minshall, 1988, unpublished observation.

[3]E. D. Koch, 1988, personal communication. Idaho State University, Pocatello.

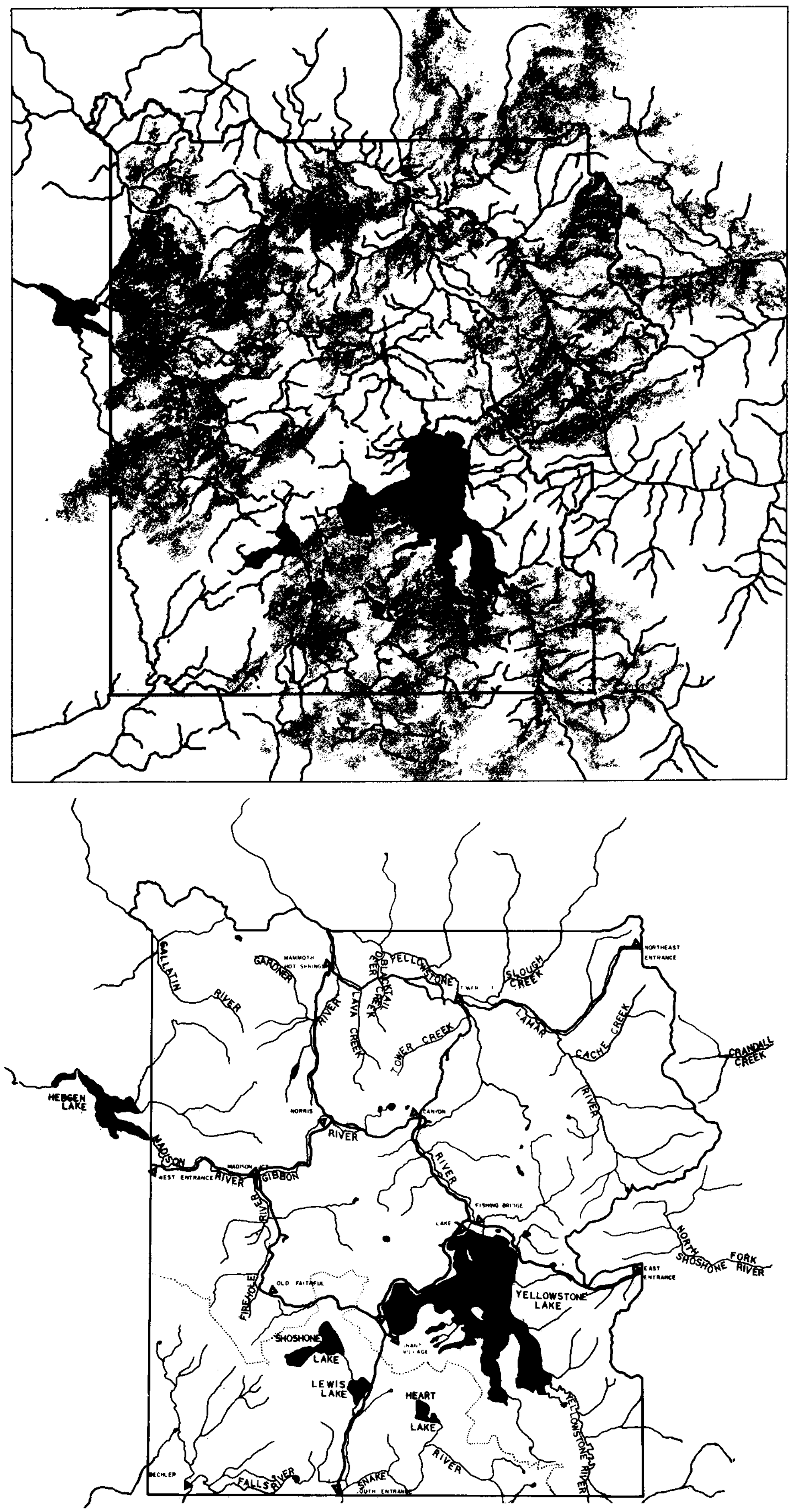

Figure 1. a. Extent of 1988 GYA fires by drainage basin. b. Names of lakes and streams. Data from Burned Area Survey Team 1988.

dead fish were observed in some second- and third-order streams in Yellowstone,[4] which may have been due to increases in certain ions from ash entering the water (Cushing and Olson 1963). In these areas, the fire may have burned more intensely and thoroughly than did those fires previously studied (Schindler et al. 1980). In addition, increased pH may act directly on aquatic organisms or may enhance the toxicity of certain substances, such as ammonia. In some cases (e.g., Little Firehole River), significant fish mortality resulted from accidental drops of ammonium phosphate, a fire retardant, into aquatic habitats.[5]

Midterm effects. The secondary consequences of fire on aquatic ecosystems in GYA may be separated into midterm and long-term effects. Midterm effects are those exerting their maximal impact within the first few years after a fire. Most of the adverse midterm delayed effects are likely to be due to increased sediment levels and turbidity and erosion of stream channels (Minshall and Brock in press). Delayed detrimental influences on water chemistry generally are prevented by chemicals becoming diluted, being taken up by plants, and binding to soil, roots, and debris.

Although moderately burned watersheds may show little or no change in stream chemistry, the combustion of living and detrital plant biomass disrupts nutrient cycling, and the watershed can lose nutrients via stream runoff. Several studies report increased nutrient runoff after wildfires or logging and slash burning (Brown et al. 1973, McColl and Grigal 1975). Other researchers suggest that microbial uptake and absorption on soil particles prevents nutrients from entering aquatic systems (Johnson and Needham 1966). We expect that for several years after the Yellowstone fires, nutrient output (Figure 2) will increase, because terrestrial plant uptake will be reduced and there will be increased mineralization and leaching of elements accumulated in the watershed.

Incident solar radiation initially increases sharply as a result of the fire due to removal of overstory vegetation, and it gradually diminishes as this vegetation recovers (Figure 2). Increased solar radiation reaching the water after a fire can elevate summer stream temperatures as much as 8–10° C (Brown 1971, Burton and Likens 1973, Helvey 1973). These increases may have a detrimental effect if they exceed critical threshold levels for resident invertebrate or fish populations. However, it is more likely that the slight (2–4° C) increases expected in most cases (Albin 1979), coupled with the increases in light and nutrients, will increase primary and secondary production, including growth of algae, invertebrates, and fish (Murphy et al. 1986, Noel et al. 1986, Wallace and Gurtz 1986). The algae (and subsequent fauna) are expected to retard the downstream movement of nutrients.

These after-fire conditions in severely burned watersheds may result in enhanced production of algae for two to six years, particularly in headwater streams. Low-order streams, which were formerly dependent on exogenous sources for their organic energy, can be expected to shift to autotrophy until riparian communities develop sufficiently to provide shade and adequate litter for a return to dependence on allochthonous (terrestrially derived) organic material (Cummins 1974, Minshall 1978).

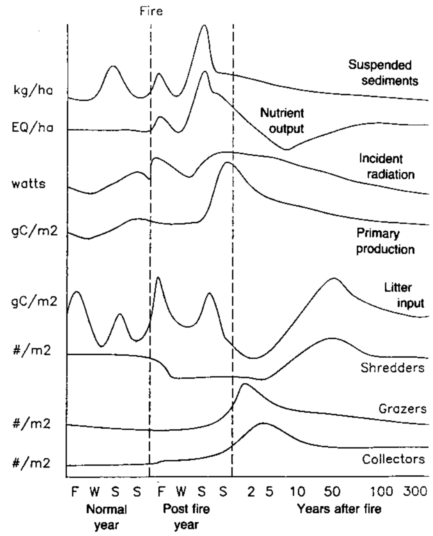

Figure 2. Projected stream ecosystem responses to a wildfire. These hypothetical trajectories illustrate anticipated changes in key physical and biotic factors. Immediate and long-term effects are illustrated by using a logarithmic scale on the abscissa after the first postfire year. Actual values depend on watershed size and edaphic influences such as watershed aspect, slope, bedrock geology, severity of fire damage (intensity and areal extent), and climatic factors such as precipitation and temperature.

Long-term effects. Most of the long-term responses of Yellowstone aquatic ecosystems to the 1988 fires (Figure 2) are likely to be closely allied with the recovery of the forest and understory vegetation (Figure 3; Hynes 1975, Likens and Bilby 1982, Minshall et al. 1985, Molles 1982, Vannote et al. 1980). Eventually, recovery of the forest cover should result in increased shading of streams and decreased runoff and input of nutrients, returning conditions in these habitats to prefire levels. Even within a region the size of the GYA, factors that regulate forest succession, such as elevation and climate, may cause streams to differ in their long-term responses to disturbance from wildfire.

ORGANIC DEBRIS DAMS. Dams of organic debris, incorporating pieces of large wood, serve to retard the downstream movement of particulate organic matter and inorganic sediments (Bilby 1981, Likens and Bilby 1982, Megahan 1982, Megahan and Nowlin 1976). Consideration of the fate of wood in streams of forested watersheds after large-scale disturbances (wildfire or intensive logging) indicates that the diameter and mass of woody debris, and hence its ability to help retain particulate organic matter, should increase progressively with successional development of the forest (Likens and Bilby 1982, Molles 1982).

Large amounts of woody debris accumulate in old-growth forest streams. Because of its high moisture content, most of this material remains intact even after hot fires and is rapidly augmented by branches and trunks brought down by the fire (Figure 4). This material remains in place unless sufficiently high discharges flush out all but the most stable pieces.

Although fallen fire-killed snags continue to accumulate in streams for 20–25 years after a fire, the new growth (through early to middle im-

[4]See footnote 1.
[5]See footnote 2.

mature forest; Figure 3) in the riparian forest contributes little woody debris (Lyon 1984). Work by Golladay and Webster (1988) suggests that increased stream nitrogen levels, greater invertebrate abundance on woody substrates, and greater stream channel instability may break down woody debris faster in the first few years after a fire than at other times. As the forest matures and natural thinning occurs, additional woody material, increasing in diameter and mass, accumulates in streams. This process accelerates as old-growth forest conditions are attained, and standing stocks of wood in the stream return to prefire levels.

Retention of woody debris is a direct function of the size of the material relative to the width and depth of the stream. Smaller streams begin to recover to prefire levels of wood debris sooner than larger streams, and the frequency of debris dams decreases with increasing stream size (Likens and Bilby 1982). In the GYA, the pattern shown in Figure 4 is most appropriate for headwater through third-order streams; significant woody debris accumulations are absent in most streams greater than fourth order.

SUSPENDED SEDIMENTS. Suspended-sediment yield (Figure 2) is normally positively correlated with water discharge, and in the Rocky Mountain region sediment yield follows the general pattern of snowmelt runoff (Bjornn et al. 1977). Mass movement (movement of a portion of the land surface, as in creep, landslide, or slip), wind, and rain are expected to produce an increase in sediment concentration in the months immediately after a fire. Snowmelt runoff is expected to carry abnormally high suspended-sediment loads, which decrease annually as the watershed becomes revegetated (Megahan et al. 1980). Unusually high spring runoff or intense summer thunderstorms after the first year could cause short-term departures from this decreasing trend.

Increased sediment erosion into streams draining burned watersheds, as well as the elevated suspended-sediment levels, invariably result in increased sedimentation in downriver depositional areas. As the burn site revegetates and erosion diminishes in the years after a fire, the deposited fine sediments in mountain streams are expected to be progressively transported downriver by spring runoff. This sequence was observed for the south fork of the Salmon River in Idaho after cessation of logging activities (Megahan 1975, Megahan et al. 1980).

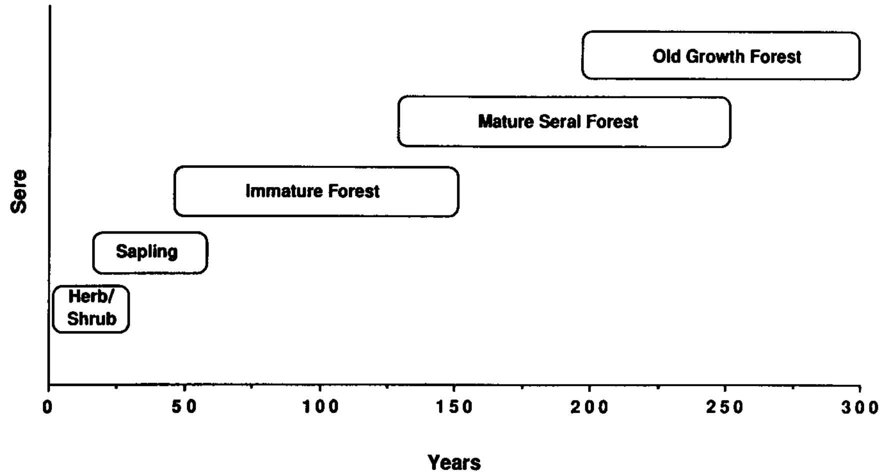

Figure 3. Succession in lodgepole pine (*Pinus contorta*) forest after wildfire (after Arno et al. 1985, Romme 1982).

NUTRIENT CYCLING. The initial nutrient pulse is expected to be followed by a gradual decrease in nutrient loss from the watershed, concomitant with high recovery of net photosynthetic rates of terrestrial vegetation (Bormann and Likens 1979). Low nutrient concentrations in the stream 5–10 years after the fire (Brown et al. 1973) are expected to contribute to the decline in autochthonous (within the stream) production.

Although the effect of enhanced light levels in increasing primary production should persist 10–20 years (Hansmann and Phinney 1973, Hawkins et al. 1983, Murphy et al. 1986, Newbold et al. 1980, Noel et al. 1986), low nutrients may override the stimulatory effect of increased light. For example, in Carnation Creek, logging increased the amount of light reaching the water, but primary and secondary production remained limited by low phosphorus (Culp and Davies 1983, Shortreed and Stockner 1982). During later forest succession, we expect nutrient export levels to drop below prefire levels as competi-

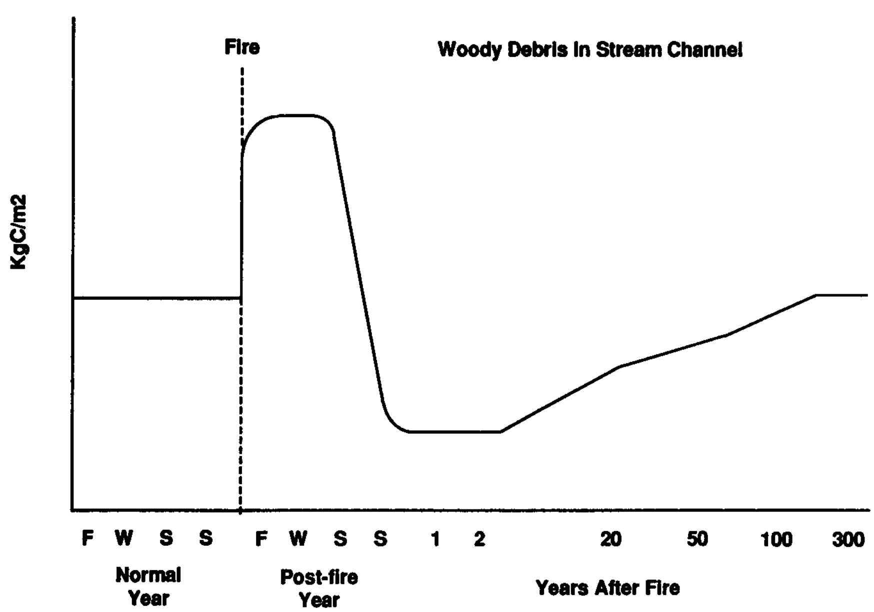

Figure 4. Postulated response of woody debris in lodgepole pine forest after wildfire.

tion among plants for nutrients intensifies and nutrients accumulate in plant biomass (Bormann and Likens 1979).

The changing nutrient and light regimes are expected to shift temporarily the benthic flora from diatoms and moss to green algae, with brief (2- to 5-year) development of filamentous algal mats (e.g., *Cladophora*). Albin (1979) found no difference between attached algae accumulations in unburned sites and those burned 36 and 45 years previously, thus supporting the pattern shown for recovery of primary production in Figure 2.

Streams should be efficient at retaining nutrients after fires, and the degree of response depends on stream order (Grimm 1987, Meyer 1980, Meyer and Likens 1979, Minshall et al. 1983b, 1985, Newbold et al. 1982, 1983, Vannote et al. 1980). With increasing stream order, the riparian canopy is likely to have a progressively declining effect on instream ecosystem dynamics (Vannote et al. 1980). Most nutrient uptake and growth of algae and other organisms is expected to occur in first- and second-order streams, and little effect of wildfires will be seen with respect to light and nutrient dynamics in streams larger than approximately fourth order. A major exception to this generalization may be the influx of nutrients from tributaries into streams that are fourth order or larger (Minshall et al. 1985).

The two major factors affecting the pattern of dissolved nutrient concentrations in streams are water-borne transport and biotic uptake and release (Minshall et al. 1983b, Newbold et al. 1982). Biotic processes appear to be more important in regulating phosphorus, nitrogen, and potassium, whereas discharge (volume of water per unit time) and related geologic processes are thought to exert the dominant regulatory force on calcium, magnesium, and sodium ions (Henderson et al. 1978). In GYA, physical transport is most important during spring runoff and sporadic summer rain storms, and biotic uptake peaks at midsummer.

In streams in the western United States, the most important nutrient regulating the primary producers often is nitrogen (Grimm and Fisher 1986). Therefore, it is expected that nitrogen entering GYA streams from the watershed will be taken up rapidly and retained tightly by the system (Grimm 1987, Newbold et al. 1983). It also is likely that nitrogen will markedly influence the rate of litter decomposition (Meyer and Johnson 1983). The nitrogen effects on both primary producers and litter decomposition can control secondary production in streams (Grimm 1988).

Measurements from Cache Creek in YNP shortly after the 1988 fire indicate a progressive decline in nitrogen concentration with distance downstream[6] (Figure 5). The greatest change (sixfold) occurred between first- and second-order sites, and then a twofold decrease was observed at each of the subsequent shifts in stream order, continuing through the confluence of Cache Creek with the Lamar River. These results indicate substantial and differential uptake of nitrogen along the course of the stream, even though October is a period of declining light and temperature. The most significant variation in this downstream pattern should occur as a result of the entrance of tributaries draining burned watersheds. We expect the lower-order, nutrient-laden tributaries to stimulate biotic production in the receiving streams for some distance downstream of their confluence. This biostimulatory response should significantly retard the downstream flush of nitrogen. However, severely decreased light levels, due to suspended sediments during storm runoff, could counteract this nutrient enrichment effect.

Organic litter input. Organic litter input to the land and stream, including export to and retention by the flood plain adjacent to the stream during runoff, will be elevated during the first year after the fire, but then it will decline as the forest community returns (Figure 2). There is experimental evidence (Otto and Svensson 1981) that aquatic herbivores may be sensitive to differences in secondary compounds in vascular plants. Thus far, the topic has been examined only from the perspective of the coevolution of aquatic grazing invertebrates versus aquatic and riparian plants. Given the aquatic invertebrates' demonstrated ability to distinguish between closely related aquatic and terrestrial plants, it seems quite feasible that changes in secondary compounds in terrestrial vegetation in response to fire could result in changes in the quality of allochthonous leaf litter entering streams, which would affect its use by aquatic detritivores. Because allochthonous detritus is a primary determinant of energy and organic-matter dynamics in streams (Hynes 1975), any significant changes in its quality or quantity are likely to exert profound effects throughout the stream ecosystem.

Stream fauna. Responses of the benthic invertebrates to the aftermath of the Yellowstone fires are expected to vary depending on the degree of sedimentation (Hawkins et al. 1983) and streambed movement that occurs. Increased flows, streambed erosion, and high suspended-sediment concentrations for major snowmelt or rainfall runoff pulses in the first year after the fire may bring about massive invertebrate drift out of streams draining the burned areas. Deposition of fine sediments also may cause diminished invertebrate standing crops in those habitats affected. For example, heavy accumulations of fine sediments will eliminate the mixed gravel-cobble substrate preferred by endemic species, causing recovery to be delayed until sediments are eroded and the benthos is recolonized.

Recolonization of these depopulated areas will depend on the extent of fire-induced disruption of upstream headwater areas, which will serve as seed sources. From previous work conducted on the Teton River in Idaho (Minshall et al. 1983a), we predict that recovery may take three years or more, depending on the severity and extent of scouring due to runoff.

Benthic invertebrates can be divided into groups on the basis of their feeding behaviors. These categories are called functional feeding groups and are expected to respond differently to the effects of fire. They include shredders, which consume streamside, riparian litter after it enters the stream; collectors, which use small particles of organic matter in the water; and grazers (scrapers), which eat attached organic matter, especially algae.

[6]See footnote 2.

During recovery from a fire, shredder populations (Figure 2) are expected to be almost entirely absent due to the destruction of quality leaf litter sources by the fire. Grazer density should increase after fire, following a pattern similar to that of primary production, on which they directly feed (Murphy et al. 1986, Noel et al. 1986, Wallace and Gurtz 1986).

Once a productive autotrophic community becomes established, amounts of high-quality benthic organic matter will be elevated, thereby enhancing collector populations, although some species may be eliminated due to the higher summer temperatures. Higher levels of transported organic material from both terrestrial (rapidly growing herbaceous and shrubby plants) and in-stream sources (sloughed periphyton and invertebrate feces) will bring about increased densities of filter feeders (a subcategory of collectors), most notably caddisflies (Hydropsychidae, Brachycentridae) and blackflies (Simuliidae). Collector densities consequently will exceed prefire levels during the intermediate postfire years due to elevated levels of endogenous organic material.

As postfire plant regrowth occurs and the canopy closes, we expect to see a shift in the predominant food from algae to terrestrial leaves and needles (Figure 2). High quality (fast decomposition) herbaceous litter, consumed first by shredders and then by collectors, should gradually be replaced by lower quality (slow decomposition) deciduous leaves, which in turn will be supplanted by even lower quality conifer needles and twigs (Figure 3). For example, Molles (1982) postulated that, during postfire forest succession, the recovery of Trichoptera shredders would parallel the accumulation of conifer wood and forest litter in streams. Over time, the shredder populations are expected to recover, whereas those of the grazers will decline to prefire levels.

Further, we expect that the number of debris dams will increase progressively during the first 25 years (Figure 4), resulting in increased retention capacity for allochthonous food resources. For example, Molles (1982) found five times the number of logs in conifer forest streams as compared to aspen forest streams and attributed the order of magnitude difference in detritus standing crop in the conifer streams to this difference in retention capacity. Likewise, Rounick and Winterbourn (1983) found that enhanced physical stability of the stream bed resulted in increased retention of allochthonous inputs and standing crops of shredders and elevated rates of leaf breakdown. Thus, as algal production declines due to reduced light and nutrient availability and as detrital standing crops increase with increasing litter and deadfall accumulations, a shift from low to high shredder:grazer ratios is to be expected (Molles 1982).

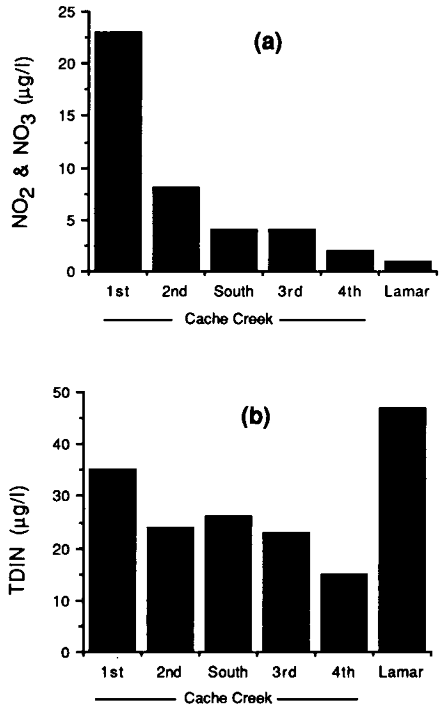

Figure 5. Nitrogen concentrations (mg/l) in Cache Creek, YNP, approximately two weeks after its watershed burned in 1988. **a.** Nitrite plus nitrate. **b.** Total dissolved inorganic nitrogen.

Potential responses to different degrees of disturbance

Fires of a magnitude such as burned during 1988 in GYA can have sweeping effects on the ecology of streams. The extent of the near-term effects of fire on stream ecosystems and the rates of return to prefire conditions are dependent largely on the degree of disruption of the watershed and stream channel in the first few years after fire. The difference (for a given environmental region) appears to be due primarily to the size of the watershed burned and the intensity of the fire. However, the chance occurrence of intense summer storms, common in the Yellowstone area, also is a factor.

In Figure 6, some potential responses to different degrees of disturbance resulting from fire are illustrated for biotic features such as abundance and richness. Three alternative trajectories are illustrated:

- Those streams that because of the smaller fire-affected catchments, greater water retention by the surrounding watershed, or sheer chance avoid high intensity, scouring discharges, will begin the recovery process relatively quickly. In such cases, the stream ecosystems are expected to return relatively rapidly to prefire conditions.
- In those streams in which the watershed becomes heavily eroded and the bed severely scoured, recovery will be delayed and may ultimately follow a different trajectory altogether.
- In severe cases, such as when repeated disturbances of the stream channel occur over a long time, new, lower levels for abundance and richness may be established.

Research needs and opportunities

Although we can speculate on the effects of fires on aquatic ecosystems, insufficient specific information is available to reliably predict their effects over the array of conditions found in GYA. Conditions in aquatic habitats during or immediately after a fire have been documented in only a few cases. Little is known of the factors responsible for the observed fish mortalities, the extent of that mortality, or whether other groups of organisms also were affected.

Previous studies often differ markedly in climatic and topographic conditions from those found in GYA and the other large national parks and wilderness areas of the northern Rockies. Reports of "no adverse effect" in previous studies commonly are clouded by an inadequate database or by unsatisfactory sampling, which may have begun after the disappearance of organisms killed by the fire. Likewise, the effect of fire retardants on aquatic habitats, the downstream extent of the effect, and even the extent of the problem are poorly known.

The near-term effects of fire are probably the best described, but these studies have concentrated on chemical conditions in the water. Information on the effects of fires of different degrees of severity on the composition and productivity of algae, invertebrates, and fish are largely undocumented. Little also is known of the internal functional responses of aquatic ecosystems to fire. For example, there is considerable evidence that biological processing and physical retention may serve to retard the downstream movement of nutrients and their loss from a watershed and that these processes may vary with stream size (e.g., Grimm 1987, Minshall et al. 1983b, Newbold et al. 1982, 1983), but these ideas have not been tested.

The lack of information concerning the effects of fire on aquatic ecosystems is especially important for large-scale and long-term situations. Yellowstone offers some especially exciting opportunities for such research. For example, virtually nothing is known of the sequence of events that may occur in aquatic ecosystems after the first year or two after a fire, whether these sequences may differ from one situation to another, or what factors would be responsible for such differences.

Rarely in the history of modern ecology has the opportunity been available to examine the effects of fire on stream habitats in watersheds larger than third order or to compare responses of stream ecosystems to mosaic burns versus nearly complete, intense burns. Because of the scale of the 1988 fires and the variety of stream types and conditions represented, GYA could serve as an excellent natural laboratory for testing ideas and for supplying much-needed information for evaluating current fire management policies, predicting the effects of fire, and planning resource management strategies for stream ecosystems.

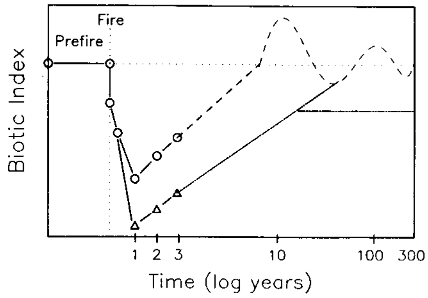

Figure 6. Expected changes in total abundance (numbers or biomass) or species richness after wildfire (from Minshall and Brock in press). Three possible recovery trajectories are shown: circles and dashed lines represent moderate impact and rapid return to prefire conditions; triangles represent relatively severe impact, eventually returning to prefire levels (dashed lines) or attaining a new (lower) equilibrium level (broken horizontal line). The actual pattern of recovery will be determined largely by the extent of disturbance of the watershed and stream channel from runoff in the first few years after the fire.

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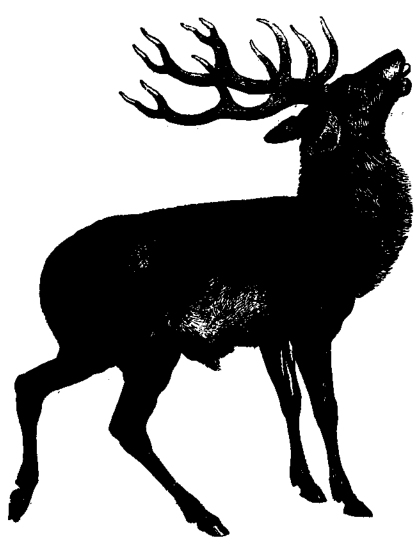

Drought, Fires, and Large Mammals

Evaluating the 1988 severe drought and large-scale fires

Francis J. Singer, William Schreier, Jill Oppenheim, and Edward O. Garton

Yellowstone National Park is renowned for its fauna of diverse and numerous large mammals. There are hundreds of black and grizzly bears (*Ursus americanus* and *Ursus arctos*) that roam the area, and coyotes (*Canis latrans*) and mountain lions (*Felis concolor*) as well, but ungulates far outnumber them.

Approximately 2500 bison (*Bison bison*) inhabit the park in three herds (Meagher 1973, 1988). There are also approximately 2500 mule deer (*Odocoileus hemionus*), 400–500 pronghorn antelope (*Antilocapra americana*), 250–400 bighorn sheep (*Ovis canadensis*), and 200 moose (*Alces alces*) on Yellowstone's northern winter range.

In winter, four herds of elk (*Cervus elaphus*), approximately 22,500 individuals in 1988, inhabit the park and adjacent areas that are part of the northern winter range (Figure 1). Elk from five other herds migrate into the park each summer, increasing the population to approximately 31,000.[1] This article focuses on elk, because they are overwhelmingly the dominant park ungulate both in number and total mass. In early 1988 on the northern winter range, there were five times as many elk as all other types of ungulates combined.

Fires directly killed few elk, but the fires and drought increased the next winter's die-off

Since the designation of Yellowstone National Park (YNP) in 1871, elk management there has been controversial. Early park managers held an almost agricultural philosophy for ungulate management, which included artificial feeding of elk, bison, and pronghorn antelope; elimination of wolves (*Canis lupus*); and near elimination of mountain lions (Weaver 1978).

By 1911, some concern was expressed about the increasing number of elk. This concern grew after a large winterkill of elk in the park in 1919–1920 (Cahalane 1941, Skinner 1928) and intensified further during the severe drought of 1919–1936.[2] Artificial reductions of park elk, bison, and pronghorn were then conducted; however, the killings were terminated in 1968 after a public outcry and congressional hearings.

Cole (1971) and Houston (1976) proposed experimental management of the elk and bison based on the premise that, over a period of years, native ungulate populations would regulate their own birth and death rates in relation to available winter food and population size. A natural regulation experiment has continued for the park elk and bison herds from 1968 to the present. Cayot et al. (1979), Despain et al. (1986), and Houston (1982) reported the experiment to be largely successful, although Beetle (1974) and Chase (1986) have argued that elk numbers are still increasing and the elk are diminishing the vegetation.

At the time of the 1988 drought and fires in Yellowstone, studies of the northern range were reevaluating the success of the natural regulation experiment. Extensive burning in 1988 occurred on five out of the seven elk summer ranges. All four of the elk winter ranges had from 2–50% of their areas burned. No previously published study has documented burning effects on such a large scale across the entire year-round ranges of several large elk herds.

Drought effects on grasslands

Summer weather conditions in 1988 significantly reduced grassland productivity, although earlier in the year there was no water shortage. We counted and measured height of vegetative leaves and reproductive stalks for three key elk forages: bluebunch wheatgrass (*Agropyron spicatum*), prairie junegrass (*Koeleria cristata*), and Idaho fescue (*Festuca idahoensis*). Measurements were taken on all

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[1] F. J. Singer, 1989, manuscript submitted.

[2] M. Coughenour and F. J. Singer, 1989, manuscript submitted. Colorado State University, Fort Collins, and Yellowstone National Park, WY.

Table 1. Effects of the 1988 drought on grasses on Yellowstone's northern range. The warmer-site grasses were reduced more than grasses growing in the Lamar Valley, which is located at the cooler, upper reaches of the winter range.

	Percent change over 1986 and 1987			
Grass species	Leaf number	Flower number	Tallest leaf	Tallest flower
Warm-site grasses				
Agropyron spicatum	−24	−12	−28	−25
Koeleria cristata	−48	−54	+23	−6
Lamar Valley				
Agropyron smithii	+74	−23	−12	
Festuca idahoensis	+100	+18	+25	
Poa spp.	+77		−7	

the grass clumps within ten randomly located one-meter-square plots. This data was compared to similar measurements gathered in 1986 and 1987.

The low winter snowpack during the winter of 1987–1988 set the stage for dryer than normal conditions in early 1988 (Table 1). Precipitation during the winter of 1987–1988 was only 31% of normal. However, April and May 1988 precipitation was 168% of normal, and as a result grass growth in the cooler Lamar Valley was at least as good as in 1986 or 1987 (Table 1).

The months of June, July, and August were among the driest on record for the Yellowstone area (averaging 36% of normal precipitation). Temperatures were also elevated. (June temperatures were 5° C above normal, and July was 0.5° C above normal.) Above-average winds also contributed to the dryness. Warm-site grasses were significantly reduced by the 1988 drought (Table 1). Summer range grassland production values were reduced more than 50%.[3] Typically elk still find green forbs and grasses in forest stands in September, and frequently late rains stimulate fall greening in the open grasslands. August and September of 1988, however, were so dry that elk ate primarily dried grasses.

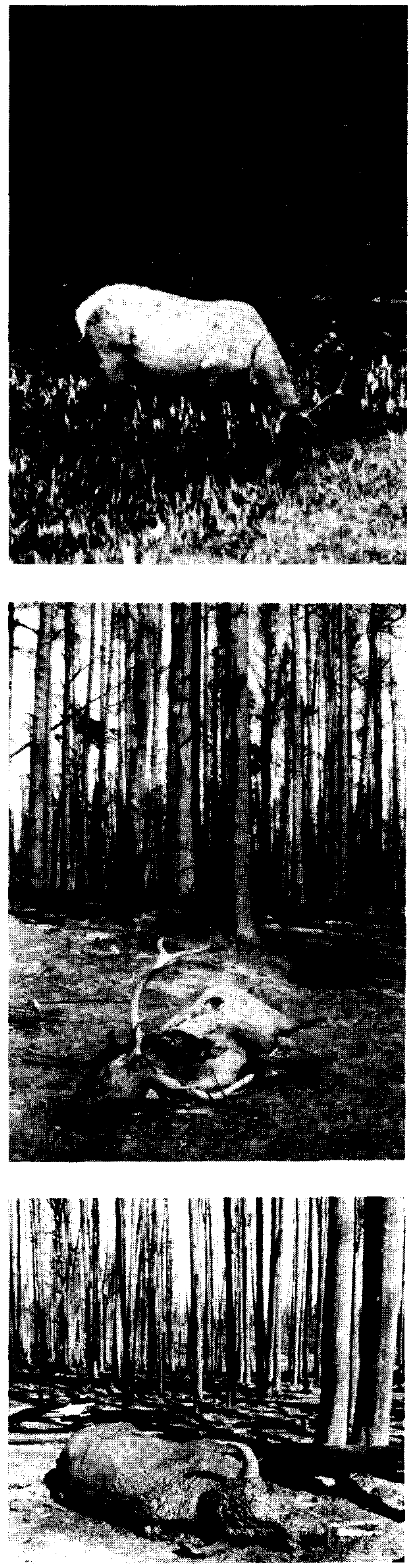
Fire mortality

Immediately after the fires began to subside, we surveyed fire-caused large mammal deaths in 15 burned areas where wide, fast-moving fire fronts occurred (Figure 2). Helicopters were used to survey transects 0.4 to 0.6 km apart, and in six of the burned areas an additional 694 km were surveyed by foot and horseback. Trachea and muscle samples were collected to determine whether the animals had died of smoke inhalation.

A total of 261 large mammals were found dead in the areas of four of the 1988 fires within Yellowstone National Park: 246 elk, 2 moose, 4 mule deer, and 9 bison. This count represents approximately 1% of the 31,000 elk summering within YNP and an even lower fraction of the other animals. None of 68 radiocollared park elk died in the fires. Two radiocollared grizzly bears in the park are believed to have been killed by the fires (Blanchard and Knight in press); the proportion of the grizzly bear population possibly killed is estimated at 0.5–1%. An additional 137 large mammals were killed just outside of the park (89 elk, 10 moose, 6 black bear, and 32 mule deer).[4]

We suspect the count includes all the large groups of carcasses in the park. The more than 10,000 fire fighters, who accumulated 18,000 flight hours and more than 1000 km of foot travel, reported carcasses. In addition, the large carcass piles were especially noticeable as they were visited by hundreds of scavenger birds and animals. Small groups of one to three carcasses may have gone undetected.

There is almost no published documentation of large mammals dying in



Elk (top) grazing in a burned forest. Elk (center) and bison (bottom) carcasses found after the fire.

[3]E. Merrill and L. Wallace, 1989, personal communication. University of Wyoming, Laramie, and University of Oklahoma, Norman.

[4]T. Kilough, G. Roby, D. Tyers, 1988, personal communication. Wyoming Game and Fish Department, Cody and Jackson, WY, and US Forest Service, Gardiner, MT.

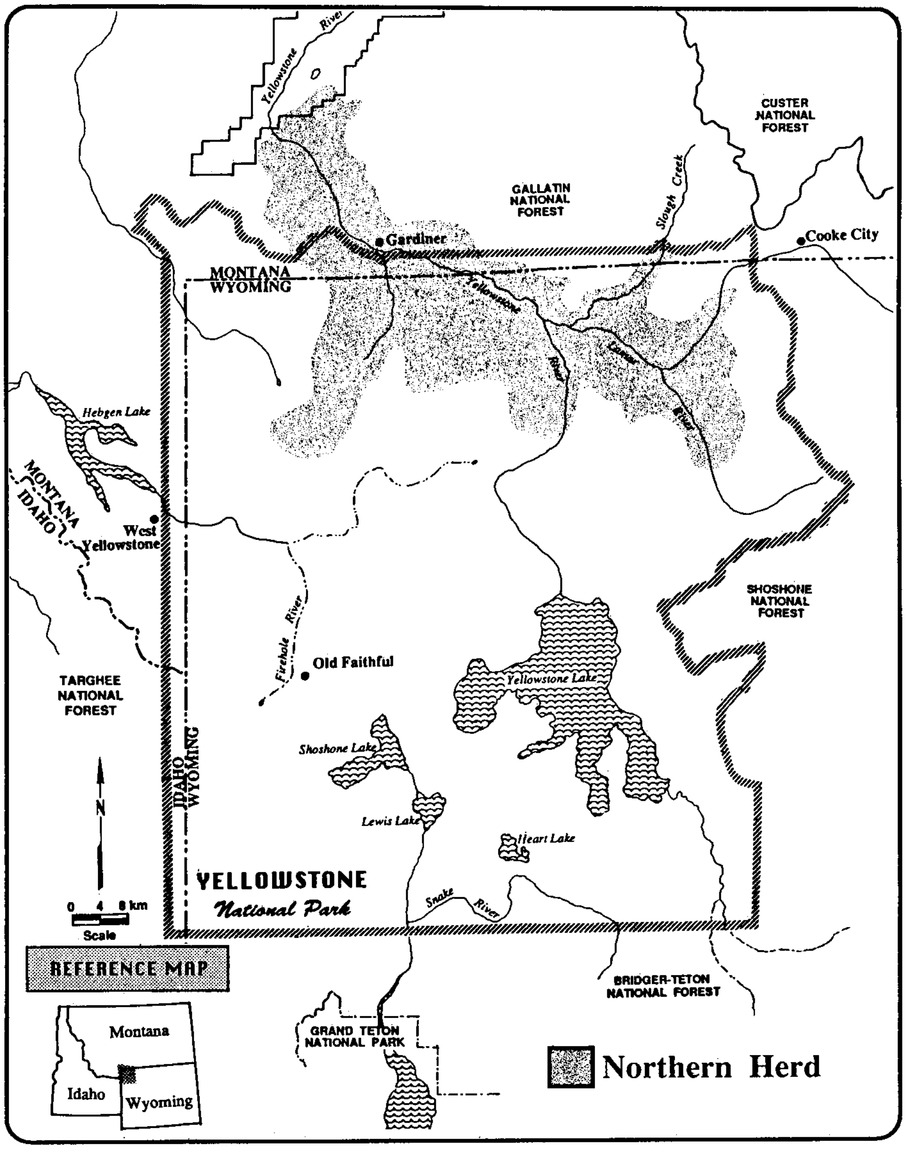


Figure 1. Winter range for the northern Yellowstone elk herd.

either wildfires or prescribed burns in North America (Bendell 1974, Buckley 1958, Howard et al. 1959, Leege 1968), although large mammals, including elephants (*Loxondonta africana*) and antelopes have occasionally been observed to be killed by fires in Africa (Komarek 1969). Chew et al. (1958) reported a fire-killed black-tailed deer (*Odocoileus hemionus*) in California. In general, elk and other large mammals have proved adept at avoiding flames and moving around fire fronts.

Groups of carcasses contained 1 to 146 dead elk. Generally the sizes, sex and age composition, and locations of dead elk were suggestive of typical rutting group aggregations of cows, calves, and yearling bulls, with a central harem bull and several competing large bulls in satellite positions. The only exception was a large group of 146 elk, found clustered in a 20-meter circle, which we speculate consisted of several harem groups that had bunched together in panic.

Sex and age ratios of the fire-killed elk were 36 calves, 11 yearling bulls, and 63 adult bulls per 100 cows. The calf and yearling bull-to-cow ratios did not depart significantly from the herd ratios as a whole; however, more adult bulls died in the fires than expected based on the herd ratio (chi-square test, $\chi^2 = 25.63$, $p < 0.002$). Cow-calf groups tend to use open habitats more than bulls do (Geist 1982, Lieb and Marcum 1979). Therefore, the greater preference for cooler, mature forests on north and east slopes (Geist 1982) where fires burned faster, and perhaps the solitary nature of mature bull elk in summer, may have made bulls more vulnerable than cow-calf-yearling bull groups.

Trachea evidence suggests smoke inhalation killed all or nearly all the fire-killed elk before they were burned by the flames. Twenty-five of 30 tracheae examined contained caked soot below the level of the vocal cords (Moylan 1980, Walker et al. 1981). Four tracheae were completely burned, precluding examination, and in another specimen, the trachea lining was absent.[5] Dense, low-lying smoke was observed in front of several fires at the approximate time of the elk deaths.[6] One group of elk south of the park was killed when caught between the Mink fire and a man-started back burn.[7] Flames burned or singed most of the elk carcasses, especially ears, hooves, teeth, hides, and shattered antlers. The bodies of some suffocated elk in small wet sites, however, were unburned.

Topography and aspect significantly influenced the distribution of fire-killed elk (Kolmogorov-Smirnov test, $p = 0.03, 0.04$; Figures 3 and 4), but slope did not ($p = 0.42$; Figure 5). Sixteen (41%) fire-burned elk groups, and 47% of the elk carcasses, were on mountain sides or ridgetops, 10 (26%) were on level or rolling terrain, and 13 (33%) were in creek bottoms. Most of the dead elk in the creek bottoms were lying in water or were only 2–3 m from the water, suggesting they sought the water or the lowest local point, where the smoke would have been less thick.

The only known injured survivors of the fires, a mature bull elk and bison, sought refuge in the Lava Creek bottom. The bison died the day after the fire, but the bull elk survived for 42 days before it was found and disposed of humanely. The bull elk had severely burned hide on the hips and lower legs, and its hooves were

[5]S. P. French, 1989, personal communication. Yellowstone Grizzly Foundation, Evanston, WY.

[6]R. Barr, 1988, personal communication. Yellowstone National Park, WY.

[7]G. Roby, 1988, personal communication. Wyoming Game and Fish Department, Jackson.

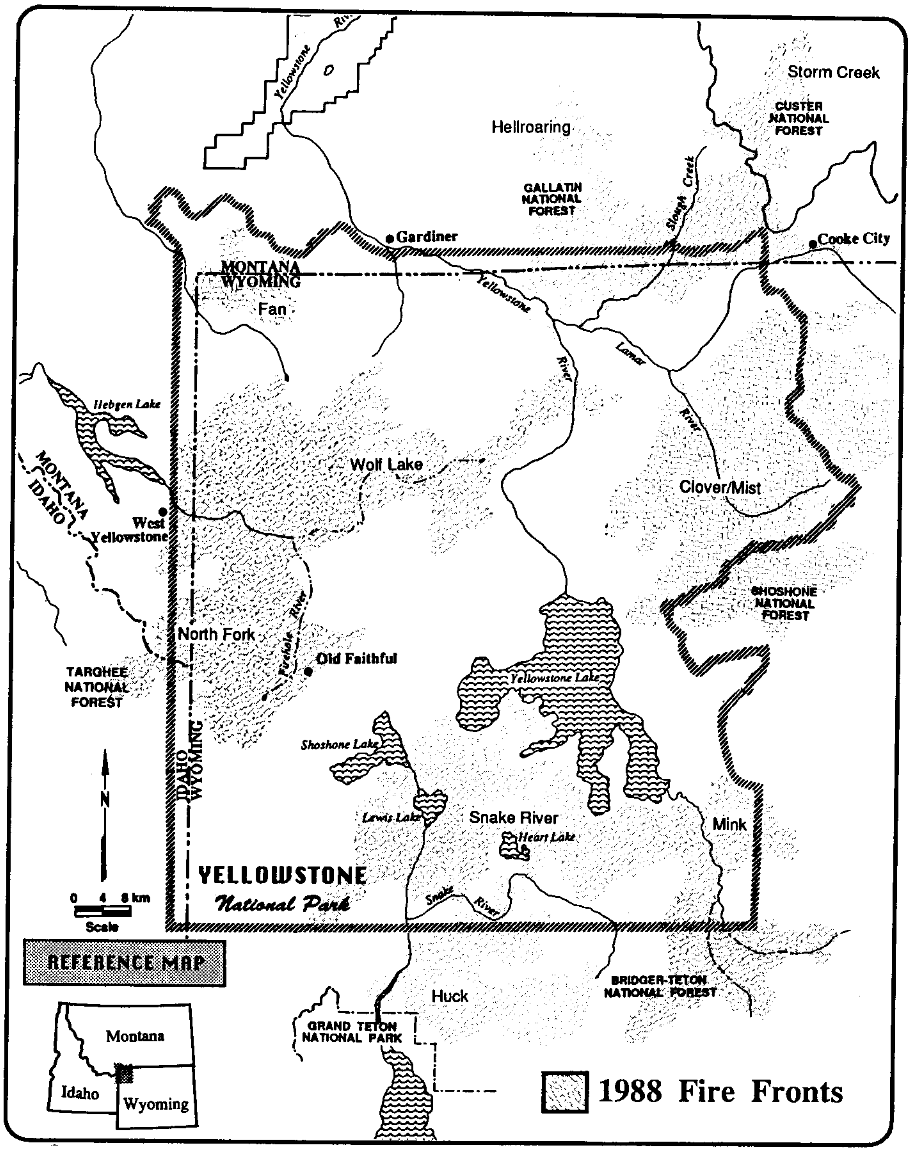


Figure 2. Major fronts of fire complexes in Yellowstone National Park in 1988.

partially burned off. It had not moved more than 30 m since the fire and was surviving on greening streamside sedges (*Carex* spp.).

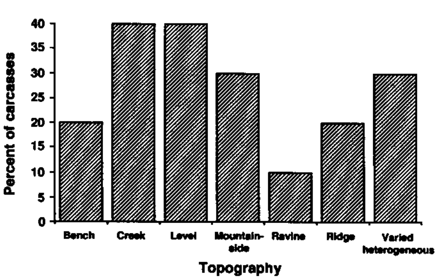


Figure 3. Percentage of elk carcasses killed by the 1988 fires in various topographic sites.

Seven of the fire-killed groups of elk (18%), and 30% of the elk carcasses, were found in open grasslands, usually on the edge of a forest (Figure 5). The remaining 33 groups (82%) were in conifer forest, including 10 in whitebark pine stands (*Pinus albicaulis*), 8 in mature lodgepole pine stands (*P. contorta*), 7 in mid-aged lodgepole, 3 in young lodgepole forests, 3 in spruce-fir forests (*Picea* spp. and *Abies lasiocarpa*), and 2 in Douglas fir (*Pseudotsuga menziesii*) stands (Figure 5).

The dead large mammals were all found in sites where sustained wind speeds of 10–20 kilometers per hour (kph) with gusts to 60 kph were documented during the fires and where

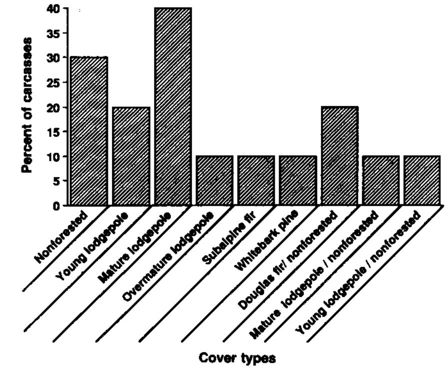


Figure 4. Cover types where fire-killed elk carcasses were located during 1988.

the estimated rates of fire spread were 4.1–6.9 km/hr.[8] No large-mammal mortality was observed in fires where slower rates of fire spread were estimated and the animals could move out of the way. Fire fronts exceeding 2 km in width and total fire runs of 6–21 km in a day were characteristic of the sites where large-mammal mortality occurred.

Scavenging activity on the fire-killed carcasses was extensive, and nearly all the carrion was consumed by 1 December 1988 (Figure 6), 82 days after the last known fire mortality. At least 600 ravens (*Corvus corax*), 30 bald eagles (*Haliaeetus leucocephalus*), and a large number of grizzly and black bears and coyotes (*Canis latrans*) used the carcasses. The ungulate contribution to the grizzly bear diet increased to 27% in 1988 from an average 8% in 1979–1987 (Blanchard and Knight in press). Raven activity was observed at 54% of the carcasses, coyote activity at 29%, grizzly bear activity at 27%,

[8]P. Perkins, 1989, personal communication. Yellowstone National Park, WY.

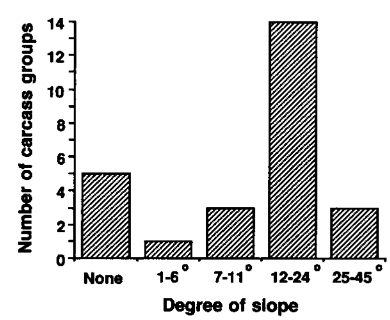


Figure 5. Slopes where fire-killed elk carcasses were located during 1988.

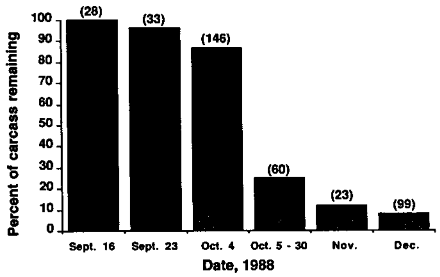


Figure 6. Consumption of fire-killed elk carcasses by scavengers during 1988.

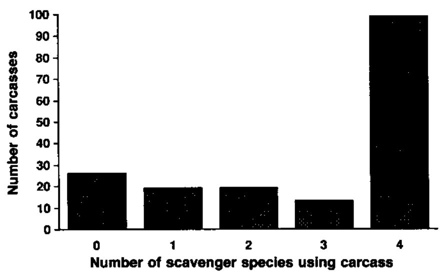


Figure 7. Number of scavenger species known to use fire-killed elk on the basis of signs at the carcasses.

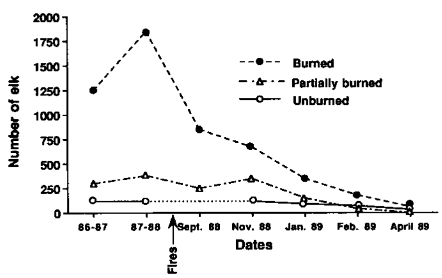


Figure 8. Numbers of elk observed in burned, partially burned, and unburned study areas on Yellowstone's northern range after the fires of 1988.

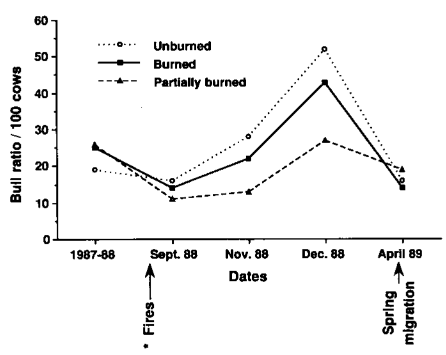


Figure 9. Ratios of bull to cow elk on burned, partially burned, and unburned study areas during the winter after the fires of 1988.

black bear activity at 7%, and eagle activity at 7%. More than one species of scavenger used many of the carcasses (Figure 7).

Elk distributions

Elk numbers and winter distributions have been assessed each year since 1985 by two or three aerial surveys of the entire northern winter range. Monthly monitoring was conducted during the winter of 1988–1989 on three watershed study areas: unburned (Rose Creek), approximately half burned in a mosaic pattern (Amethyst Creek), and mostly burned (Blacktail Deer Creek). A sightability correction factor was based on sightings of 34 radiocollared elk (Samuel et al. 1987). A step-wise logistic regression analysis equation was used to evaluate the effect of the following factors on observability of elk groups: percent tree cover, group size, and observer.[9]

Elk moved to winter ranges four to six weeks early in 1988, apparently in response to both the drought and the fires. Elk also migrated from the park in larger numbers than in recent years. An estimated 54% of the northern herd migrated across park boundaries, where approximately 18% of the winter range exists but where no fires burned. This large migration was probably related to the drought effects on forage abundance, the burning of winter ranges, and a heavy snowpack. The winter of 1988–1989 was only the third time since 1916 that more than one-half the herd migrated from the park (Houston 1982). One of these winters, 1919–1920, also followed a summer of severe drought.

In November 1988, normal numbers of elk occupied the unburned and partially burned study areas, but only 45% as many occupied the burned study area (Figure 8). Proportionately more animals left the burned and partially burned study areas as the winter progressed. Even in burned areas, elk in early winter were able to find alternate forages such as the bark from downed, burned, but still-green aspen trees (*Populus tremuloides*), unburned grasses and sedges from mesic depressions that did not burn, and sedges that became green again after the fires from sites that did burn. But as snows deepened, these limited forages became much less accessible.

Proportionally fewer mature bull elk than cows left the mostly burned, or partially burned, study areas immediately after the fires (Figure 9); the unburned study area is located in the upper portions of the winter range where snow is deepest. Because they remained in greater numbers in these areas, bulls died at higher rates than cows; by late winter, bull ratios in the northern herd were only 18 bulls per 100 cows compared to a typical ratio of 30 per 100 (1986–1988; Figure 10).

McCullough (1969) argued that bull elk are subjected to a higher mortality rate than cows due to energy depletion and injuries associated with the rut and also due to greater movement rates. Our observation that older bulls are less likely to migrate from burned winter ranges is contrary to this argument and the proposals of Mitchell et al. (1977), who along with Geist (1982) hypothesized that bull elk are less loyal to established home ranges than were cows. Flook (1970) observed bulls to colonize new habitat before cows did, suggesting that bulls are less loyal. Calf elk are also more vulnerable to winterkill than are cows (Figure 10). By late winter, only 7 calves per 100 cows were left alive, compared to a typical late winter ratio of 20 calves per 100 cows.

Winterkill in 1988–1989

Carcasses of winterkilled elk were counted using a helicopter on a set of random sites comprising one-third of

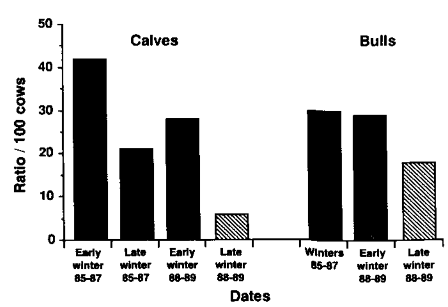


Figure 10. Calves and bulls per 100 cows in Yellowstone's northern elk herd after the fires of 1988.

[9]F. J. Singer and E. O. Garton, 1989, unpublished data.

Table 2. Ungulate population responses to the fires of 1988 and the 1988–1989 winter, Yellowstone National Park, WY.

Ungulate population	Percent of winter range burned: Dry grassland	Wet meadow	Forest	All types	Early count	Corrected estimate	Spring 1989 count	Corrected estimate	% Herd reduction	Known harvest	Carcasses counted	Estimated number of carcasses
Elk												
Upper Yellowstone-Thorofare	0	55	26	50	461	—	57	—	Migrated	—	—	—
Madison-Firehole	15	27	38	41		—	199	—		tr	330	469–667*
Northern	8	1	11	34	10,908	17,207–19,059†	8739	11,801–13,137†	38–43	2773	1004	3021–5757‡
Mule deer	0	0	0	0	2217	—	1796	—	19		—	—
Pronghorn	0	0	0	0	473§	—	372	—	27	49	—	—

*Estimate based on a helicopter count and correction factor for half of the winter range; 264 dead elk were directly counted in the other half of the winter range by ground crews of the Interagency Grizzly Bear Study Team.
†Sightability estimates following Samuel et al. (1987).
‡Estimate based on a helicopter count of one-third of the area (in 22 count units randomly selected from 66). The helicopter count was corrected by a simple ratio estimator (5.46 ± 1.7) calculated by comparing helicopter to ground counts (representing nearly total counts) on 13 small study plots of 3–12 km^2.
§D. Scott, 1989, unpublished data. Yellowstone National Park, WY.

the entire northern range. A correction factor for the efficiency of the helicopter surveys was established through intensive ground survey of 13 sample plots of 5–14 km^2. Similar ground and helicopter surveys were conducted in the Madison-Firehole winter range.

A group of elk from the North Fork Shoshone herd, which typically winters in what was the most severely burned winter range in the upper Yellowstone-Thorofare area, apparently migrated to the east. An early winter count conducted in the burned winter range was 461, but only 57 elk were counted in January 1989 (Table 2). Elk winterkill in the Madison-Firehole winter range, where fire had affected 41% of the area, was approximately 50%. The northern Yellowstone elk herd declined 38–43% during the winter of 1988–1989, of which 14–16% were harvested by humans and another 24–27% were killed by natural forces. During the mild winters of 1986–1987 and 1987–1988, elk mortality was less than 5%.

Houston (1982) reported that in the severe winter of 1974–1975, 10% of the northern herd died. He made no correction for carcasses not seen and therefore may have underestimated the winterkill. Park staff reported that 60% of the northern herd died in the severe winter of 1919–1920, which followed the drought of 1919. Houston (1982) later questioned the accuracy of their estimates, but we believe a large winterkill occurred.

Mule deer and pronghorn antelope were less affected by the fires of 1988, because none of their winter range burned and their population changes during the winter of 1988–1989 more directly reflect a response to the drought and the winter conditions. Mule deer counts declined 19%, and pronghorn counts declined 29% (Table 2).

Projections

The elk remaining likely lost significant amounts of body weight, which could not be recovered by the time of calving. Therefore, we predicted calf weights and survival would be reduced (Thorne et al. 1976). In 1989, we found that calf weights were reduced 1.7 kg (17%), and the initial (first six weeks) calf mortality rate was twice that of previous years.[10]

Herbaceous and shrub production will likely increase in the burned areas (Lyon and Stickney et al. 1976). Protein content and palatability also will likely increase in the forages returning on burned areas (Spalinger 1986). Most forages will recover almost immediately, because root sources are still alive in most cases beneath 2.5 cm of soil.

Elk in Yellowstone have been observed to consume many forages in burned areas that were ignored before burning, apparently due to increased palatability. Leege (1968) and Keay and Peak (1980) have observed that less palatable shrubs received increased use by elk and mule deer after fires.[11]

[10]F. Singer and A. Harting, 1989, unpublished data. Yellowstone National Park, WY.
[11]D. Despain, 1988, personal communication. Yellowstone National Park, WY.

Increased body size and improved condition of adults and increased calf survival are predicted for 1990. Although the positive effects of the fires on grasses and herbs may be short-lived (Hobbs and Spowart 1984, Wood 1988), lasting perhaps only two to three years, the structural and successional changes to lodgepole forests on the park's higher plateaus are expected to create additional elk summer range for as many as 30 years. These changes are expected to include more sunlight reaching the forest floor, creation of small meadow openings, a greatly increased herbaceous and shrub layer, and higher palatability of forages. Elk diets will likely be more diverse due to the projected increases in deciduous browse available to elk. Summer home ranges of elk and movements in burned or mosaic-burned areas are likely to be smaller than before burning, as a result of the increased plant productivity. We predict that the size of the park's elk herds will likely increase as a result of the 1988 fires, depending on the severity of winter conditions during the next few years.

Research opportunities

The fires of 1988 have provided a unique opportunity to observe the responses of extensive populations of large mammals to large-scale fire, including the ranges of several large herds, and to test several research and management hypotheses. The fires directly killed only 1% of the elk, but the combined effect of drought and fire was a large die-off during the following winter. The hypothesis that the fires greatly enhanced the future range carrying capacity for the northern herd may now be tested. Aspen and willow communities have existed largely in the absence of fires since the mid-1800s (Houston 1973). We can now see what effect fire has on the vigor and heights of sprouts and to see if fire-stimulated sprouts escape the height of elk browsing.

Houston (1982) has hypothesized that precipitation influences grassland dynamics on the northern range more than do elk numbers. Grassland data from 1989 can provide a test of this hypothesis, because wet conditions (24% above normal precipitation January–June) followed severe drought and the intense grazing pressure that peak elk numbers exerted on the ranges in winter 1988–1989.

The fires of 1988 also have provided the opportunity to observe the effects of fall burning on forage abundance, forage quality, and nutrient flows on a large ecosystem scale. The fires may enhance the spatial and landscape relationships of water, cover, and forage areas. An alternative hypothesis is that the quality and quantity of summer range was not limiting before the fires and the effects of the fires will be relatively minor.

Elk selectively forage for high-quality diets even in variable environments (Baker and Hobbs 1982). For example, Rowland et al. (1983) found no difference in quality of winter diets of elk between burned and unburned Ponderosa pine (*Pinus ponderosa*)–bunchgrass types in New Mexico, and Canon et al. (1987) also found no diet quality or species composition difference in elk diets between burned and unburned aspen types in Wyoming. Canon and his colleagues, however, did conclude that elk forage efficiency was greater in the burned areas as measured by bites per minute, average bite size, and travel time while foraging. The fires of 1988 will also provide the opportunity to see if Yellowstone's largely unhunted northern elk herd will naturally regulate its numbers if there is, as hypothesized, rapid population growth after the fires.

The Yellowstone fires offer unique opportunities to address important research questions. We can observe the consequences of fire throughout the ecosystem, from microbes to large mammals. It is important to set up research programs immediately to follow long-term aspects of the recovery process.

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