

The Yellowstone Fires

A Primer on the 1988 Fire Season



National Park Service
Yellowstone National Park

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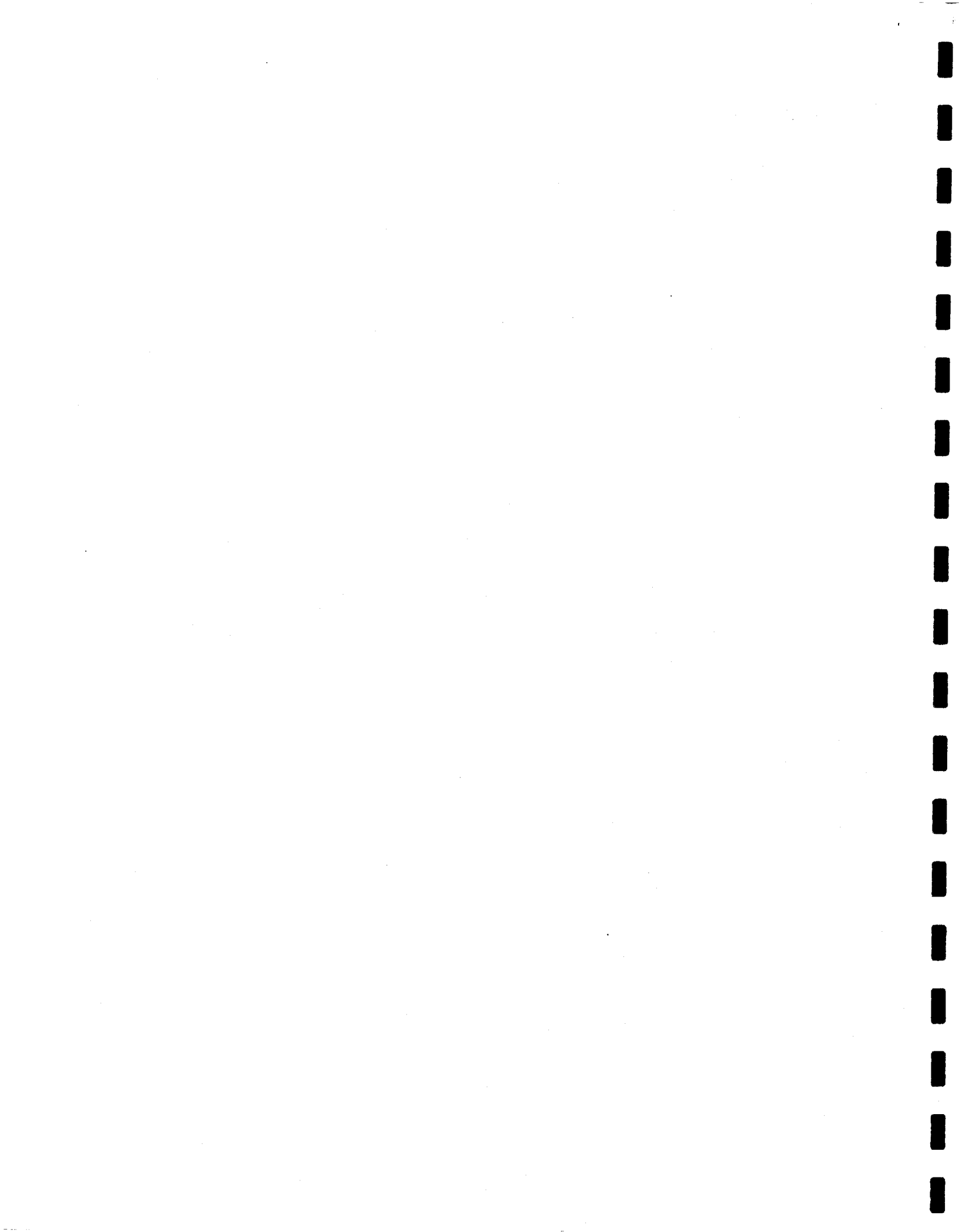


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INTRODUCTION

The Greater Yellowstone Area fires of 1988 have received more national attention than any other event in the history of the parks, and are already being described as the cause of the largest fire suppression effort ever undertaken in this country. The fires have provided compelling evidence of the power of nature, and have generated renewed interest in the parks and their management. Fighting the fires has required all of the attention of the concerned agencies, so that no comprehensive overview of the whole fire story has been possible. This summary has been prepared for use until more complete reports are available.

This summary provides a brief overview of the Yellowstone fire situation as of October 1, 1988. Eventually complete fire histories will be assembled for all Yellowstone fires. In the meantime, the present narrative should serve to introduce the essential information. Statistics presented here should be regarded as preliminary and may have to be revised later as more complete information is received on various fires.

The bracketed numbers in the narrative refer to a variety of publications, information papers, and working reports produced during the fire that are appended to provide in-depth information.

Additional information will be available from the Superintendent, Yellowstone Park, Wyoming, 82190, 1-307-344-7381.

YELLOWSTONE'S FIRE PREHISTORY AND HISTORY

Naturally caused fires have occurred in the Yellowstone area as long as there has been vegetation to burn--at least since vegetation appeared following the retreat of glaciers about 12,000 years ago [1,2]. Fire, climate, erosion, and a vast assortment of life forms ranging from microbes to insects to mammals have all played roles in the creation of the vegetative landscape of Yellowstone.

The process was still going on when humans first arrived. During several thousand years of intermittent occupation of the Yellowstone area, native Americans may have influenced the vegetation in many ways, such as setting fires (accidental or intentional), moving seeds (in plant foods or horse's feed, for example), or influencing the

numbers or movements of various plant-eating mammals.

The arrival of European man heightened human influence on vegetation, primarily through suppression of fires that would have burned unimpeded in earlier times. After the park was established, in 1872, park managers gradually improved their ability to monitor and control fires. Virtually no effective fire fighting was done until 1886, when the U.S. Cavalry was placed in charge of protecting the park. In fact, these soldiers marked the debut of federal involvement in fighting wildfires in the United States. The army, which did not leave Yellowstone until 1918, successfully extinguished some fires, though it is difficult to determine what effect their efforts had on overall fire frequency or extent.

In these early days, fire suppression was most effective on the grasslands, shrublands, and savannas of the park's northern range; fires were not allowed to burn freely on the grasslands and groves of the northern range for nearly a century [3]. Over the rest of the park, which is largely covered by forest, reliable and consistent fire suppression had to wait until modern airborne firefighting techniques became available, in the last thirty or forty years [4].

YELLOWSTONE'S FIRE MANAGEMENT PLAN

At the same time that we were learning more about putting fires out, a sense of the importance of natural processes was also increasing. Starting in the 1960s, managers in many national parks attempted to restore as much of the primitive setting as practical [5]. Step by step, Yellowstone's wildness has been given greater respect and freedom. Thus, in the 1930s, predators such as wolves, cougars, and coyotes were no longer controlled, in recognition of their possible role in the population dynamics of the park's herbivores; after the 1950s, hot springs were no longer channeled from their natural courses into swimming pools; in the 1960s black and grizzly bears were divorced from a variety of human food sources, and elk and bison population numbers, long pruned, were permitted to reach levels in keeping with available habitat; and in the 1970s the park's fisheries management program was redirected to restore high quality angling while restoring depleted fisheries populations. Many of these management actions were or continue to be controversial, and are the subject of ongoing research and evaluation.

Ecologists have known for many years that wildfire is essential to the evolution of a natural setting; when fires are suppressed, normal plant succession processes are stagnated, and biological diversity is reduced or altered. Research into Yellowstone's prehistory has shown that on the park's northern range fires occurred one to four times a century, while over the vast extent of the park's subalpine forests the fire interval was more typically 200 to 400 years. Nature has lots of time, and at either interval fire was a premier force (along with climate and soils) in determining vegetative cover in what would become the park. The legislative mandate of the National Park Service is to maintain as near as possible a primitive ecological situation, and so it was that in the 1960s and early 1970s interest grew in restoring the influences of fire to the park [6].

On most public and private lands, of course, maintaining wild processes is not as high priority as other activities, such as grazing stock, harvesting timber, or providing recreation. On such lands, permitting wildfire to burn may be no more appropriate than trying to maintain a population of grizzly bears on a commercial sheep ranch. But in natural areas such as Yellowstone, preserving a state of wildness is a primary goal of management.

In 1972, Yellowstone was one of several national parks that initiated programs to allow some natural fires to run their courses. That year 340,000 acres, in two backcountry units, were designated as appropriate for naturally caused fires. The plan was developed and implemented after substantial communication with related agencies, and with the endorsement of the conservation and scientific communities. In 1974, after the initial successes of the program, plans were made to expand the acreage. In 1975, an Environmental Assessment was prepared on allowing fires to burn on about 1,700,000 acres in the park; the E.A. was approved early in 1976, and shortly thereafter Yellowstone Park and the Bridger-Teton National Forest entered into a cooperative program to involve the Teton Wilderness in the fire plan, so that naturally caused fires could burn across the boundary between the two federal units.

Over the years since 1976, Yellowstone's fire management plan has been gradually revised and updated in accordance with National Park Service guidelines. In 1986 a new revision of the plan--really just a refinement of earlier plan editions--was completed, and was in the final stages of approval as of the spring of 1988.

All park fires, whether man-caused or natural, are managed according to criteria in the fire management plan. Natural fires are continuously monitored, and tactics for monitoring and possible control are updated daily. Fires that threaten adjacent public or private lands and communities, park developments, or other significant resources, are suppressed with the same effort applied to fires on other public lands.

Yellowstone's fire management plan has four goals:

1. To permit as many lightning-caused fires as possible to burn under natural conditions.
2. To prevent wildfire from destroying human life, property, historic and cultural sites, special natural features, or threatened and endangered species.
3. To suppress all man-caused fires (and any natural fires whose suppression is deemed necessary) in as safe, cost-effective, and environmentally sensitive ways as possible.
4. To resort to prescribed burning when and where necessary and practical to reduce hazardous fuels, primarily dead and down trees.

Scientists have learned much about the occurrence and behavior of fire during the sixteen years since this plan has been put into effect. Tens of thousands of lightning strikes simply fizzle out with no acreage burned. Of those that have occurred in the past sixteen years, 140 produced fires. Most burned only a small area, but a few larger fires were started, so the average burn size was 250 acres. Eighty percent of the lightning starts in this period went out by themselves.

During this sixteen-year period, a total of 34,175 acres burned in the park due to natural fires [7]. The largest natural fire burned about 7,400 acres. During these years we lost no human lives and had no significant human injuries due to the fires. No park structures or special features were affected.

The largest natural fire in the park's written history prior to 1988 was a burn at Heart Lake in 1931. It was fought, but burned about 18,000 acres.

Fire was permitted to reassert its role in creating and maintaining the natural variety of habitats and vegetation

types typical of a healthy wilderness, and millions of visitors had the opportunity to observe this fascinating natural process in operation.

THE FIRES OF 1988

Conditions

The summer of 1988 has been the driest on record in Yellowstone. April rainfall was 155 percent of normal, and May rainfall was 181 percent of normal, but practically no rain fell in June, July, or August, an event previously unrecorded in the park's 112-year written record of weather conditions. In early summer, about 20 lightning-caused fires had been allowed to burn [8]. According to the fire plan, fires were evaluated on a case-by-case basis, each on its own situation and merits, before being allowed to burn. Eleven of these burned themselves out, behaving as such fires did in previous years.

But those that survived into the extremely dry weeks of late June and July met dramatically changed conditions. By late July, moisture content of grasses and small branches in the park reached levels as low as two or three percent, and down trees was measured at seven percent (kiln-dried lumber is 12 percent). At 8 to 12 percent, lightning will start lots of fires, many of which will burn freely. At 12 to 16 percent, some fires will burn to 200 to 300 acres. At greater than 16 percent, there are still some starts, but few will burn any significant amount. Twenty-four percent is saturation. A series of unusually high winds, associated with dry fronts, fanned flames that even in the dry conditions would not have moved with great speed.

Yellowstone experienced an untypical weather pattern in recent years. Though there was below-average precipitation in winter, summers were abnormally wet, sometimes reaching 200 to 300 percent of normal rainfall in July. The recent statistics on rainfall in summer are striking enough to merit listing here:

Percent of normal rainfall

	April	May	June	July	August
1977	10	96	63	195	163
1978	91	126	42	99	46
1979	6	17	42	115	151
1980	33	152	55	143	199
1981	49	176	102	103	25
1982	169	74	89	118	163
1983	22	29	69	269	88
1984	44	84	66	297	121
1985	42	93	44	160	84
1986	145	47	64	212	75
1987	42	144	72	303	122
1988	155	181	20	79	10

Anticipating the continuation of this pattern, park managers and fire behavior specialists saw reason to expect that natural fires could be allowed to burn. Six consecutive years of significantly above-average July rainfall suggested that July of 1988 would be similarly wet.

Fighting the Fires

By July 15, however, it was clear that recent weather patterns were not of use in predicting this summer's weather. As of that day, the perimeter of fires in the park was about 8,600 acres. After that day, no new natural fires were allowed to burn. Exceptions were made for natural fires that started adjacent to existing fires, when the new fires were clearly going to burn into existing fires. After July 21, all other fires were also subjected to full suppression efforts as manpower would allow. As of that day, the perimeter of the fires in the park totalled less than 17,000 acres. On July 27, during a visit to Yellowstone, the Secretary of the Interior reaffirmed that the natural fire program had been suspended and all fires would be fought. Man-caused fires had been vigorously suppressed all along.

An extensive interagency fire suppression effort was initiated in mid-July in the Greater Yellowstone Area, to attempt to control or contain an unprecedented series of wildfires. The extreme weather conditions and heavy, dry fuel accumulations presented even the most skilled professional firefighters with conditions rarely observed.

Accepted firefighting techniques, such as constructing fire lines along the edges of the advancing fires to create

fuel breaks, and backfiring to reduce fuel accumulations in front of advancing fires, were frequently ineffective because fires spread long distances by "spotting," a phenomenon by which wind carries embers from the tops of the 200-foot flames far out across unburned forest to start spot fires well ahead of the main fire. Regular spotting up to a mile and a half away from the fires made the widest bulldozer lines useless and enabled the fires to cross such major topographic features as the Grand Canyon of the Yellowstone River. Fires routinely jumped such traditionally recognized barriers as rivers and roads.

Fires often moved two miles per hour, with common daily advances of five to ten miles, consuming even very light fuels that would have been unburnable during an average season. The fast movement, coupled with spotting, made frontal attacks on the fires impossible dangerous, as fire crews could easily be overrun or trapped between a main fire and its outlying spot fires.

Even night time fires could not be fought. Normally, wildfires "lie down" at night, as increased humidity and decreased temperature quiet them; humidity remained low at night, and fire fighting was further complicated by extreme danger from falling trees.

Fire fighting efforts were directed at controlling the flanks of fires and protecting lives and property in the advancing paths of the fires, and the experts on site generally agreed that without help from the weather, in the form of rain or snow, there was no technology in existence that could stop the fires.

The frustration and wonder of the firefighters at these conditions were summed up by Denny Bungarz, a U.S. Forest Service fireboss from Mendocino National Forest in California. Bungarz was incident commander on the North Fork Fire, the one that threatened Old Faithful and West Yellowstone and eventually reached the northeast region of the park. Bungarz said, "We threw everything at that fire from Day One. We tried everything we knew of or could think of, and that fire kicked our ass from one end of the park to the other." Similar sentiments were expressed by other leading firefighters.

Some media attention has been given to restrictions routinely placed on firefighting techniques in the park and in surrounding wilderness areas. In many situations, for example, the use of motorized equipment is limited or excluded in order to preserve primitive values to whatever

extent practical. Such restrictions are a matter of established guidelines, and were rarely considered a hindrance by the firebosses who ran the operations (most comments on the restrictions seem to have originated from rank and file firefighters). Contrary to media reports, bulldozers were in fact used in the park when requested by the firebosses, and fire engines were used regularly off roadways in fire suppression efforts. A complete review of these tactical matters will occur this winter.

By the last week in September, about 50 lightning-caused fires had occurred in the park, eight of which were still burning [9]. More than \$100,000,000 had been spent in control efforts on fires in the Greater Yellowstone Area, and most major park developments--and a few surrounding communities--had been evacuated at least once as fires approached within a few miles of them. At the operation's peak, nine thousand firefighters (including army and marine units), more than 100 fire engines, and dozens of helicopters from many states participated in a huge, complex effort to control the fires and at least protect developments.

As there were also many fires burning in the Greater Yellowstone Area outside the park, and because of the magnitude of the firefighting effort within the park, many agencies and organizations were involved in the effort. The fire suppression effort in the Greater Yellowstone area is the largest such effort ever undertaken in the United States. This summary cannot do justice to the logistical challenges, spectacular natural power, human drama, and sheer size of this fire season. Chronicles of many forms will certainly be produced, both within and from outside of the various agencies that took part in the fires.

Extent of Fires

No topic has caused more confusion in the media and in the public mind than the actual extent of the fires. Confusion has resulted from all fires in the Greater Yellowstone Area, which includes more than ten million acres of public land, being called "Yellowstone Park fires," from all fires in the Yellowstone area being ascribed to the park's natural fire program, and from frequent and unfortunate oversimplification and exaggeration of burn acreages.

This was an extremely difficult fire year throughout the west, and the country surrounding Yellowstone Park was

hit heavily. A number of major fires, most notably the North Fork Fire, the Hellroaring Fire, the Storm Creek Fire, the Huck Fire, and the Mink Fire, started outside the park and moved in. These fires accounted for more than half of the total burn in the Greater Yellowstone area, and include most of the ones that have received intensive media attention. The North Fork Fire, which threatened Old Faithful, Madison, Canyon, Norris, West Yellowstone, Mammoth Hot Springs, and Tower-Roosevelt Lodge, was probably started by a woodcutter's cigarette in Targhee National Forest and was the subject of immediate suppression efforts. The Storm Creek Fire started as a lightning strike in the Absaroka-Beartooth Wilderness of the Custer National Forest northeast of Yellowstone Park, and eventually threatened the Cooke City-Silver Gate area, where it received extended national television coverage and was usually reported as a result of Yellowstone Park's natural fire program.

Additional confusion results from continued media and public belief that managers in the Yellowstone area let park fires continue burning unchecked, out of devotion to the natural fire plan, long after such fires were in fact being fought. As pointed out earlier, no fires have been managed to burn since July 21. Public confusion was probably heightened by misunderstandings over just what the firefighting strategies were; if crews were observed letting a fire burn an area, it may have seemed to the casual observer that the burn was merely being monitored. In fact, in many instances firebosses recognized the hopelessness of stopping fires in certain situations, and concentrated their efforts on the protection of buildings and developed areas. The most unfortunate public and media misconception about the Yellowstone firefighting effort may have been that human beings can always control fire if they really want to; the raw, unbridled power of these fires cannot be overemphasized. Firefighters were compelled to choose their fights very carefully, and they deserve great acclaim for working so successfully to save all but a few of the buildings in the park. This was a heroic achievement.

Perhaps the worst source of confusion, however, has resulted from oversimplification of burn acreages. The daily reports issued cooperatively by the U.S. Forest Service and the National Park Service on fire status gave total acreages within the perimeters of each fire, pointing out that, "only about half of the vegetation has burned within many fire perimeters." Most reporting has focussed on the total acreage, and neglected the important statement about unburned vegetation. The park was regularly portrayed as a blackened moonscape.

The perimeter estimates are indeed shocking at first sight. Fires that started in Yellowstone Park totalled about 659,000 acres (preliminary estimate as of October 1) in and out of the park. Fires that started outside the park and moved in totalled about 969,000 acres in and out of the park. More detailed statistics will be available soon.

Because all available resources, including helicopters, were committed to fighting the fires, and because of dense smoke, it was not possible during the fires to make accurate estimates of unburned acreages within the fire perimeter. As of the last week of September, however, preliminary flights indicate that, though there is great variation from area to area, "about half" is probably not far off as a general estimate. As of October 1, the total fire perimeter (areas within which some burning occurred) within the park was about 1,100,000 acres (50 percent of the park). Approximately 440,000 acres (20 percent of the park) actually experienced some burning. Approximately 220,000 acres (10 percent of the park) experienced canopy fires only, and approximately 22,000 acres (one percent of the park) experienced high heat intensity fires.

Of the 1,100,000 acres within the burn perimeters in the park, roughly half were the result of man-caused fires.

There was substantial variation of burn acreage from fire to fire. For example, about 30 percent of the area within the perimeter of the Fan Fire burned, while as much as 70 percent of the Lava Creek, Firehole, and Madison River areas may have burned areas. Preliminary surveys suggest that about 90 percent of the burned areas received light to moderate soil heating, 10 percent received high heat, and none received extreme heat. Light to moderate heats do not customarily kill seeds and bulbs more than an inch below the surface, so Yellowstone's plant communities will be fully capable of regenerating.

Photographic mapping flights are currently underway, and more detailed surveys will be made later this fall. Resurveying the vegetation cover of more than 2,000,000 acres of national park is a time-consuming and expensive project. It may well be, when all the information is in, that only about half of the acreages now being reported as burned are actually burned. The significance of this characteristic of the burns, that they do not take everything, has as yet been unappreciated by both the media and the public; the ecological significance of the burn patterns is enormous.

Post-fire Response--Assessment and Rehabilitation

By late September, as the fires were diminishing, plans were underway in Yellowstone Park to develop comprehensive programs for all aspects of post-fire response. These will include replacement, rehabilitation, or repair of damaged buildings, power lines, fire lines, trails, campsites, and other facilities. An estimated 1,000 miles of fire lines, dozens of fire camps, tons of litter, 100 miles of roads, more than 600 miles of trails, and innumerable helispots and other local impacts will eventually require restoration. The restoration of Yellowstone's wilderness setting--that is, the healing of the necessary wounds of firefighting--will be of great importance to the National Park Service, to many members of the conservation community, and the public.

Similarly, programs are being developed to interpret the fires and their effects to visitors and to the general American public.

Yellowstone will cooperate with other agencies and state and local governments in promoting economic recovery of the communities near the park whose business was affected by the fires, including national and international contacts with the travel industry.

The scientific community, both private and public sector, has already shown great interest in monitoring the ecological processes following these major fires. The National Park Service is cooperating with other agencies and independent researchers and institutions in developing comprehensive research directions to take full advantage of this unparalleled scientific opportunity. It is probably safe to say that this research effort will be unparalleled in the history of the national parks, and its impact will be felt throughout the scientific community for many years to come.

The public has been expressing great interest in somehow helping with the Yellowstone fires and future programs involving the park's response to the fires. The National Park Service is determined to be responsive to these interests, and to find ways for all who may be interested to participate. A cooperative agreement has been entered into with the National Park Foundation, a Washington-based nonprofit institution, to serve as the main repository for contributions. For more information on contribution programs and how the public can help, contact

the Superintendent, Yellowstone National Park, Wyoming,
82190.

Yellowstone Park's Post-Fire Recovery Plan is being
developed at present, and will be available later this fall.

Ecological Consequences and the Esthetics of Fire

The fires of 1988 had an enormous effect on the Greater Yellowstone area. The face of the park and surrounding lands has been dramatically changed, on a scale not widely anticipated even among fire ecologists. But the change is not without precedent. The most recent research by Dr. William Romme, and independent Colorado fire history scientist, and his associates, still unpublished, suggests that the Yellowstone area has been visited by natural fires on this scale periodically in the past, including comprehensive burns in the early 1700s and in 1850.

The many effects of fires on wilderness processes were the subject of considerable scientific scrutiny even before 1988, as suggested earlier; this scrutiny will now expand. What is well known is that the vegetative setting of Yellowstone is in good part the product of fires that burned here freely before the arrival of European man. Each new burn initiates a sequence of events in the plant community that influences all other living forms in the area, especially in terms of the nutrient flow through the ecological systems. Fire suppression, as suggested earlier, halts or retards that flow [10].

Some plants, such as the lodgepole pine, are fire tolerant, and begin to seed in immediately following the fire, with seeds being released from both heat-sensitive cones and from mature cones-of-the-year. Park plant ecologist Don Despain has already documented seed densities in forests burned in 1988 ranging from 50,000 to 1,000,000 seeds per acre. Some of these seeds will survive the appetites of mice, squirrels, and birds, and will eventually produce a forest much like the one that burned on the site. Within five years, there may be 1,000 seedlings per acre, depending upon how much competition they face from grasses, wildflowers, and shrubs.

The growth of the new biotic community begins immediately following a burn. As mentioned earlier, temperatures high enough to kill seeds penetrate less than an inch into the soil in most places. Only under logs and deep litter accumulations, where the fire was able to burn

for several hours, does the lethal heat pulse penetrate more deeply into the soil. Where water is available, new plant growth is immediate--within a few days. In dry soils the rhizomes, bulbs, root crown, seeds, and other reproductive tissues must wait until soil moisture is replenished the following spring.

Insects not associated with the pre-burn forest begin to use the new food sources (dead trees) immediately, while others lay their eggs in the bark. Squirrels and birds make use of a variety of seeds and cones, and root stalks of many plant species resprout within a few weeks. Within a few growing seasons, the forest floor is a mat of grasses, shrubs, and flowers, and seedlings of future forests of fir, spruce, and pine appear. Plant growth is unusually lush because of the mineral nutrients in the ash and because of increased light levels on the previously shaded forest floor.

The fires of Yellowstone did not simply annihilate all life forms in their paths. Burning at a variety of temperatures, sometimes as ground fires, sometimes as crown fires, they killed many lodgepole pines and other trees, but in fact did not kill most other plants; they merely burned the tops off of them, leaving roots to regenerate.

As the fires passed, they created a vegetative mosaic of burns, partial burns, and non-burns that will now become the new habitats of plants and animals in Yellowstone. One of the most frequent comments heard from recent visitors to Yellowstone Park has been, "I didn't expect to see so much green."

This is not to understate the large acreages that were indeed burned; it is instead to suggest that the Yellowstone fires of 1988 did not do any known harm to the natural systems for which the park is being protected. For all their other effects, including substantial economic ones for the region, and the expenditure of more than \$100,000,000 in firefighting, the fires did nothing to Yellowstone that has not been done many times in the past. We may have preferred that only natural fires had burned, and it certainly would have been preferable if the process had not involved such expense and economic hardship, but the park's natural systems do not directly suffer from human economics. One of the greatest challenges offered by national parks is a conceptual one: they compel us to take the long view, and consider nature's directions rather than our own [11]. We are not protecting the parks merely for ourselves, but for many later generations, who will witness the revegetation of

Yellowstone with an interest and excitement hard to appreciate through the smoke of 1988.

And the burns will affect future fires. Vegetation capable of sustaining another major fire is quite rare for decades, except in extraordinary situations (the 1988 fires actually reburned heavily burned areas in some locations). Lightning strikes and even firebrands from fires in neighboring forests can only ignite small spots. The mosaic of young and mature plant communities provides natural firebreaks, reducing the number of fire starts and limiting fire size over time while sustaining a greater variety of plant and animal species.

Smoke, quickly moving fires, and the demands of firefighting logistics made it impossible to monitor mortalities of large mammals during the fires. Preliminary surveys in late September reveal that surprisingly few large mammals were killed by fire or smoke. Park biologists anticipated a certain amount of mortality; the fires were both extensive and fast-moving. Firefighters reported few incidents of animals involved with fires. Local rumors of large numbers of animals killed by the fires are to date unsubstantiated; extensive radiotelemetry involving more than 100 animals--elk, cougars, moose, and grizzly bears--indicates that though animal movements were sometimes affected dramatically by the passage of fires, relatively few animals succumbed, considering the large size of park wildlife populations.

As of September 29, fewer than 50 dead elk had been located throughout the Greater Yellowstone Area, and 4 bison were known killed by the fire on the park's northern range. One black bear, reportedly burned on its feet, was destroyed by a Montana State Highway Patrolman near Cooke City, and a few mule deer had been reported killed. These are only the most preliminary of numbers, and will be updated later.

Of greater significance are the short- and long-term effects of the fires on wildlife. Portions of the park's northern range burned, which may have effects on winter survival of grazing animals when coupled with summer drought conditions that reduced production of forage. In this and many other ways, fires dramatically altered the habitat and food production of Yellowstone. There is general agreement among observers that in the long run the fires created much new habitat that will serve the large mammals well [12]. The fires of Yellowstone are not an isolated event, but part of an endless process.

Wildfire has been regarded as evil in America for centuries. Though ecologists have recognized the important role of natural fire in wilderness ecosystems for more than fifty years, the general public is still largely unaware of the implications of fire suppression in wilderness. On the fundamental level of esthetics, fires still evoke a negative emotional response. Appreciation of fire is an esthetic issue, one for which the Park Service's sixteen years of natural fire experience did little to prepare the public; most Americans were unaware of the policy until the media attention this summer. Introducing Americans to the esthetic values of wildfire after the fact, so to speak, is going to be difficult, at least partly because to some it will appear that the Park Service is merely trying to put a good face on a bad situation.

And in some respects the situation is indeed bad. The great expense of the fires, coupled with considerable economic difficulties caused by the fires, cannot be simply justified in terms of the ecological health of Yellowstone Park.

But in other respects the fires cannot be judged as bad. In a naturally functioning wilderness, natural fire is neither bad nor good; it is simply a part of the process. We judge the presence of fire in a wilderness as good or bad based on our personal views of man's place in the natural world. There will never be unanimity on such a touchy topic as fire. But at all costs we should maintain a distinction between our scientific understanding of fire as a wilderness process and our personal feelings over the appropriateness of letting fires burn in national parks.

CONCLUSION

Ultimately, the greatest impacts of the 1988 Yellowstone fire season will not be ecological. Yellowstone itself is already well on its way to responding to the massive stimuli provided by the fires: natural revegetation is underway, wildlife is adapting, and winter is about to settle the last of the fires for the winter.

Far greater concern is now being expressed in many circles over the future of park management. The course of the summer's fire management raised many questions, and some management actions and policies will be challenged. Already there are debates underway about the timing of first suppression of natural fires, uses of heavy equipment in park backcountry, and related procedural matters, as well as

over the natural fire management plan itself. The entire firefighting effort will also be scrutinized as part of the necessary and routine review that must be gone through following any such huge expenditure of public funds.

The American public, management agencies, and many special interest groups now face a singular challenge: to come to grips with a newfound understanding of the power of the natural settings we are attempting to preserve and celebrate in the national parks. Beyond the operational questions of just how best to fight fires in wilderness, and beyond the policy questions of how an agency can be true to its mandate and yet anticipate an extraordinary one-in-300-year event of this sort, are deeper questions of just what we want from our parks, and just how far we are willing to let nature go in giving it to us.

Fire is one of the last great natural "public enemies." The same ecological community that decades ago taught us that predators are not bad in any intrinsic sense, and that natural diversity is as useful to human culture as a closely managed harvest, has more recently recognized that wildfire also has its values--scientific, esthetic, and even commercial. Fire is and has always been an essential part of the setting in our parks and natural areas; we cannot ignore its role, and to return to the total exclusion of it from those areas would be a folly for which our descendants would pay dearly.

Our goal in the national parks is the same as it has always been: to find some balance--some "reasonable illusion," as A. Starker Leopold so aptly put it in 1963--between the directions the natural setting might take on its own and our needs of it. We need a course of action that will permit us to appreciate fire's place and power without so wholly risking the financial and emotional disasters of the 1988 fire season. But even at that we would be well advised to retain enough humility to know that nature will not always be controlled despite our best, most carefully planned management.

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Landscape Diversity: The Concept Applied to Yellowstone Park

1

William H. Romme and Dennis H. Knight

Changes in landscape patterns may influence a variety of natural features including wildlife abundance, nutrient flow, and lake productivity. Data suggest that cyclic changes in landscape diversity occur on areas of 100 km² in Yellowstone National Park. When properly managed, large wilderness areas provide the best and probably the only locale for studying the kind of landscape changes that occurred for millennia in presettlement times. (Accepted for publication 12 May 1982)

Each successive level of biological organization has properties that cannot be predicted from those of less complex levels (Odum 1971). Thus, populations have certain attributes distinct from the characteristics of the individuals of which they are composed, and communities have unique properties beyond the attributes of their component populations. An important level of organization that is now receiving more attention is the landscape, or mosaic of communities that covers a large land unit such as a watershed or a physiographic region (Forman and Godron 1981).

The importance of large-scale landscape patterns has been widely recognized (e.g., Bormann and Likens 1979, Forman 1979, 1982, Forman and Boerner 1981, Forman and Godron 1981, Habeck 1976, Habeck and Mutch 1973, Hansson 1977, Heinselman 1973, Loucks 1970, Luder 1981, Pickett 1976, Reiners and Lang 1979, Rowe 1961, Shugart and West 1981, Sprugel 1976, Sprugel and Bormann 1981, Swain 1980, White 1979, Wright 1974, Zachrisson 1977, and others). A few studies have quantitatively treated changes in landscape patterns (e.g., Hett 1971, Johnson 1977, Johnson and Sharpe 1976, Shugart et al. 1973). We recently made a detailed analysis of landscape composition and diversity in a pristine watershed in Yellowstone National Park in relation to fire and forest regrowth following fire (Romme 1982). In this paper we describe the natural changes that have occurred in landscape

pattern over a period of 240 years and the possible consequences of these changes for certain aspects of ecosystem structure and function. Although we focus on Yellowstone in this analysis, the concepts are applicable to other ecosystems as well.

The term *landscape diversity* refers to the diversity of plant communities making up the vegetational mosaic of a land unit. Landscape diversity results from two superimposed vegetation patterns: the distribution of species along gradients of limiting factors, and patterns of disturbance and recovery within the communities at each point along the environmental gradients (Forman and Godron 1981, Reiners and Lang 1979). Both of these patterns contribute to the vegetational diversity of the Yellowstone landscape.

Over the park's 9000 km², elevation ranges from about 1800 m along the Yellowstone River in the northern portion to over 3000 m on the high peaks of the east and northwest. As a result, there are pronounced gradients of temperature and moisture, with related patterns in species distribution. The areas at lower elevations in the north support open sagebrush (*Artemisia tridentata*) parks on drier sites and aspen (*Populus tremuloides*) woodlands and Douglas fir (*Pseudotsuga menziesii*) forests in more mesic locations (Despain 1973). On the cooler subalpine plateaus one finds extensive upland coniferous forests of lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*P. albicaulis*), broken by occasional meadows and sagebrush parks on alluvial and lacustrine soils. The high peaks are covered by forests of spruce,

fir, and whitebark pine on sheltered slopes, with alpine or subalpine meadows and boulder fields on the more exposed sites. Pollen analysis of pond sediments indicates that these basic patterns of species distribution have been relatively stable during the last 5000 years (Baker 1970).

However, vegetational patterns related to the second source of landscape diversity—perturbation—have undergone changes during this time. Most of the changes have been natural, as described below, but some aspen and sagebrush communities in northern Yellowstone appear to have been altered somewhat by fire suppression during the last century. Comparisons of 100-year-old photographs with recent photographs of the same sites show that forests today are generally more dense, with an increase in conifers and a decrease in aspen, and that many sagebrush parks now contain more shrubs and fewer grasses and forbs. Streamside thickets of willow (*Salix* spp.) and alder (*Alnus* spp.) also appear less extensive and robust than formerly (Houston 1973).¹ Some have attributed these changes to excessive browsing by elk (*Cervus elaphus*) (Beetle 1974, Peek et al. 1967).

A more common explanation appears to be the virtual elimination of fire in this area from 1886 to 1975. Houston (1973) found that fires formerly recurred at average intervals of 20–25 years in northern Yellowstone, a disturbance frequency that probably was essential for the persistence of plant species and communities representing early stages of secondary succession (notably aspen and herbaceous plants). In the absence of fire, succession has proceeded unchecked and other species such as Douglas fir and sagebrush have become increasingly predominant. Thus fire

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¹Houston, D. B. 1976. The Northern Yellowstone Elk. Parts III and IV. Vegetation and habitat relations. Unpublished report, Yellowstone National Park, Wyoming.

prevention appears to have modified the overall composition of the northern Yellowstone landscape, reducing landscape diversity by increasing the area covered by late successional plant communities at the expense of early successional communities. The magnitude of this change is relatively small in the context of the entire northern Yellowstone landscape, however, since aspen and herbaceous communities comprised a small fraction of the landscape even in presettlement times (Despain 1973). Similar changes have also been described in several other western parks and wilderness areas following effective fire control (Habeck 1976, Habeck and Mutch 1973, Kilgore and Taylor 1979, Loope and Gruell 1973, Lunan and Habeck 1973). Because a major management goal in the large national parks is to preserve ecosystems in their primeval state (Houston 1971), Yellowstone recently instituted a new fire management policy that allows lightning-caused fires to burn without interference if they do not threaten human life, property, or other values (US National Park Service 1975).

The situation seems to be different on the high subalpine plateaus that dominate most of the central, western, and southern areas of the park. Because of inaccessibility, effective fire control was not accomplished here until about 1950 when fire-fighting equipment and techniques were greatly improved (US National Park Service 1975). Moreover, our research indicated that fire occurs naturally at very long intervals because of very slow forest regrowth and fuel accumulation after fire (Romme 1982). On an average site, 200 years or more are required for a fuel complex to develop that is capable of supporting another destructive fire. On dry or infertile sites, 300–400 years may be necessary. Fires ignited prior to that time are likely to burn a very small area and have a minimal impact on the vegetation (Despain and Sellers 1977, Romme 1982). Recent uncontrolled fires in the park that burned intensely in 300-year-old forests have been observed to stop when they reached a 100-year-old stand, even though weather conditions remained favorable for fire (Despain², Despain and Sellers 1977). Thus, in an ecosystem where fire historically occurred at intervals of 200+ years on any particular site, suppression during the last 20–30 years probably has had very little effect on overall landscape pattern. Any major

changes that have occurred are largely the result of natural processes that would have taken place even in man's absence.

Although the subalpine landscape apparently has not been substantially altered by man's activities (excluding, of course, those areas of intensive development for visitor use), it has by no means been static during the last 100 years. We found evidence that major fires occur cyclically, i.e., thousands of hectares may burn at intervals of 300–400 years with relatively few major fires in the same area during the intervening periods (Romme 1982). Such a fire cycle can occur because: geologic substrate, soils, and vegetation are very similar over much of the plateau region; forests over large contiguous areas grow and develop a fuel complex at approximately the same rates; and the plateau topography has low relief and few natural barriers to fire spread. Thus one extensive fire tends to be followed by another fire in the same area some 300–400 years later. In other parts of the Rocky Mountains where topographic barriers are more numerous, where succession occurs more rapidly, or where fuel characteristics are different, this particular type of fire cycle may not occur.

LITTLE FIREHOLE RIVER WATERSHED

We conducted our study in the Little Firehole River watershed, which covers 73 km² on the Madison Plateau, a large rhyolite lava flow in west-central Yellowstone. Coniferous forests predominate, with lodgepole pine occurring throughout and subalpine fir, Engelmann spruce, and whitebark pine being found on more mesic sites. Alluvial deposits in the central and northern parts of the watershed support subalpine meadows or open coniferous forests with rich shrub and herbaceous understories. The topography is generally flat or gently sloping, with an average elevation of about 2450 m.

Fire history during the last 350 years was determined using the fire-scar methods developed by Heinselman (1973) and Arno and Sneek (1977). Major fires occurred in 1739, 1755, and 1795 ($\pm$ 5 years), collectively burning over half of the upland area. Of the forested areas that did not burn at that time, nearly all were located either on topographically protected sites (ravines, lower northeast-facing slopes) that burn rarely (Romme and Knight 1981, Zachrisson 1977), or in places that had been burned by a moder-

ately large fire in 1630, less than 200 years earlier, and were covered by young forests. Since 1795 only three fires >4 ha have occurred, and all three were relatively small (<100 ha). The absence of recent large fires is almost certainly due to a lack of suitable fuel conditions over most of the watershed, not to fire suppression by man. In fact, park records show that only one fire has been controlled in this area, a 90-ha burn in 1949. The fire probably would not have covered a much larger area even without suppression, since it was surrounded by young forests and topographically sheltered sites. Today the areas burned in the 1700s support lodgepole pine forests that are all developing more-or-less synchronously: in another 100–150 years extensive portions of the watershed will again have fuel conditions suitable for a large destructive fire.

Three stages of forest regrowth following fire (early, middle, and late successional) can be recognized on upland sites. Early successional stages are usually present for about the first 40 years and are characterized by an abundant growth of herbs and small shrubs. The large dead stems of the former forest remain standing throughout most of this period, and an even-aged cohort of lodgepole pine becomes established. Middle successional stages are marked by the maturation and dominance of the even-aged pine cohort, beginning with canopy closure around 40 years and lasting until senescence around 250–300 years. Herbaceous biomass and species diversity are lowest during this period (Taylor 1973). During late successional stages (250–300+ years) the even-aged pine canopy deteriorates with heavy mortality and is replaced by trees from the developing understory to produce an all-aged, usually mixed-species stand, which then persists until the next destructive fire.

We used our data on fire history and on the rates and patterns of forest succession after fire to reconstruct the sequence of vegetation mosaics that must have existed in the Little Firehole River watershed during the last 240 years. Past landscape patterns were reproduced by first making a map showing the age (time since the last destructive fire) of all homogeneous forest units in 1978, based on extensive field sampling and aerial photography. Then, to reconstruct the landscape of 1738, for example, we subtracted 240 years from the age of each stand in 1978 and determined in which successional stage a stand of that age would

²D. G. Despain, personal communication.

have been. Where a fire had occurred more recently than the date of interest (e.g., areas that burned in 1739 in the reconstruction for 1738) we assumed that the stand was in a fire-susceptible late successional stage (Romme 1982).

Figure 1 shows the proportions of the Little Firehole River watershed covered by early, middle, and late successional stages at different times since 1738. In 1738 most of the area was covered by late successional forests, but fires in 1739, 1755, and 1795 greatly reduced the old-growth forests and replaced them with early successional stages. Middle successional stages became most abundant around 1800 and have dominated the watershed since. The early successional stages that were common in the late 1700s and early 1800s have been very uncommon since the mid-1800s. A decrease in middle successional stages after 1938 and an associated increase in late successional stages reflect forest maturation on areas burned in 1739.

To further describe historic patterns in landscape diversity, we calculated three diversity indices (similar to those used for measuring species diversity) and applied them to our landscape reconstructions for 1778–1978. We computed a richness index, based on the number of community types present; an evenness index, reflecting the relative amount of the landscape occupied by each commu-

nity type; and a patchiness index, indicating the size and interspersion of individual community units as well as the structural contrast between adjacent communities (Romme 1982). Figure 2 shows the results of plotting a weighted average of all three indices, as a measure of overall landscape diversity, and the Shannon index (Pielou 1975), which we calculated by using the proportion of the watershed covered by a community type as a measure of abundance. Both indices reveal a similar pattern: Landscape diversity was high in the late 1700s and early 1800s following the extensive fires of 1739, 1755, and 1795; it fell to a low point in the late 1800s during a 70-year period with no major fires; and it increased again during this century as a result of two small fires plus some variation in the rate of forest maturation in areas burned in 1739 and 1795. This variation in rates of succession is attributable to several factors including localized high densities of the mountain pine beetle (*Dendroctonus ponderosae*) (Romme 1982).

The dramatic changes in landscape composition and diversity in the Little Firehole River watershed during the last 240 years (Figures 1 and 2) must have been associated with significant changes in ecosystem structure and function, including net primary productivity, nutrient cycling, total biomass, species diver-

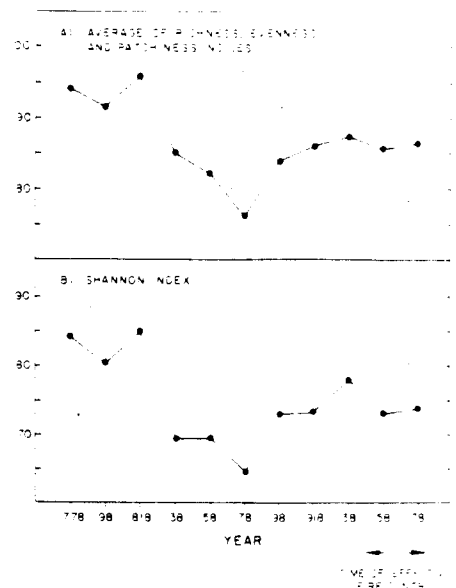


Figure 2. Changes in two measures of landscape diversity in the Little Firehole River watershed from 1778–1978.

sity, and population dynamics of individual species. These relationships cannot be fully quantified at this time, but speculation based on existing knowledge is useful.

IMPLICATIONS FOR WILDLIFE

Taylor and Barmore (1980) censused breeding birds in a series of lodgepole pine stands representing a gradient from the earliest successional stages after fire through late successional stages in the park. Their data show the pattern of avifaunal succession in a single homogeneous stand. In attempting to answer the question of how breeding bird species and populations change with time in an entire subalpine watershed, we used Taylor and Barmore's (1980) census data to estimate the number of breeding pairs in each stand within our reconstructed vegetation mosaics, summing the estimates for all to arrive at an estimate of breeding pairs in the entire watershed.

Figure 3 shows the results for three representative species and for the total number of breeding pairs of all species. Mountain bluebirds (*Sialia currucoides*) require open habitats with dead trees for nesting. Such habitat was most abundant in the Little Firehole River watershed during the late 1700s and early 1800s when 25–50% of the area was covered by early forest successional stages following the large fires of the 1700s (Figure 1). Consequently, bluebirds may have been very numerous at that time. However, as forests matured bluebird populations

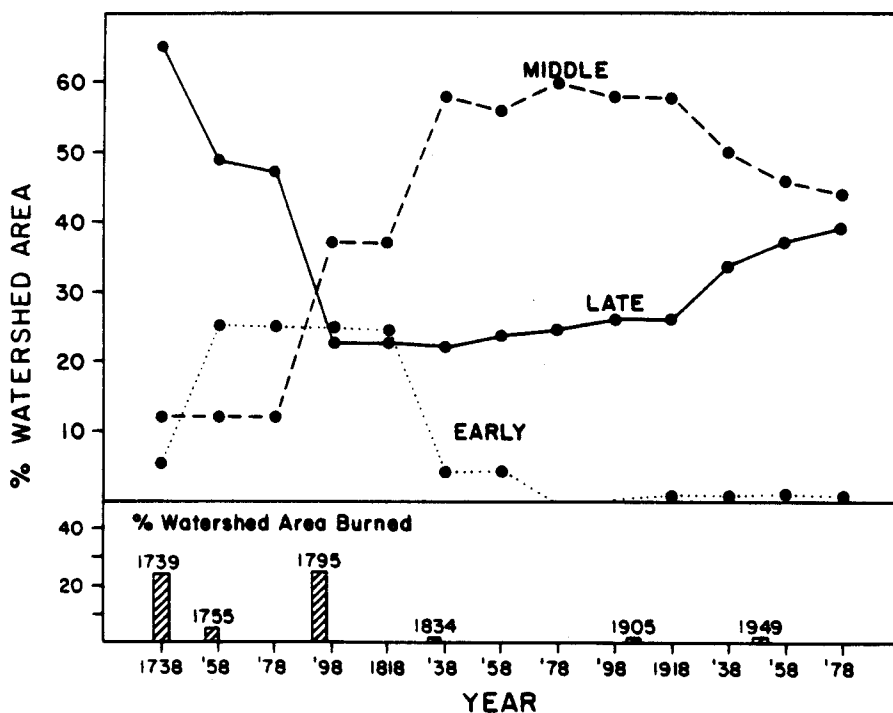


Figure 1. Percent of watershed area covered by early, middle, and late stages of forest succession from 1738–1978 in the 73-km² Little Firehole River watershed, Yellowstone National Park.

probably dropped dramatically (Figure 3). Today bluebirds are uncommon in the watershed except in the 90-ha area that burned in 1949. Note that this probable population decline was a perfectly natural event, occurring at a time when European man had not yet entered the area.

In contrast to the bluebird, ruby-crowned kinglets (*Regulus calendula*) prefer mature forests. Thus, kinglets were less common when bluebirds were most abundant (Figure 3). The yellow-rumped warbler (*Dendroica auduboni*) breeds successfully in a variety of habitats and as a result the population of this species probably has fluctuated little during the last 240 years despite the major landscape changes that have occurred (Figure 3). Figure 3 also shows that the total number of breeding pairs of all species has probably fluctuated greatly in the last few centuries. The highest numbers apparently were in the late 1700s and early 1800s when landscape diversity was also greatest (Figure 2).

The population estimates shown in Figure 3 can be challenged easily on the basis that they were derived solely from habitat availability, i.e., the number of hectares of forest present in each age class. Of necessity we have ignored other critical determinants of population

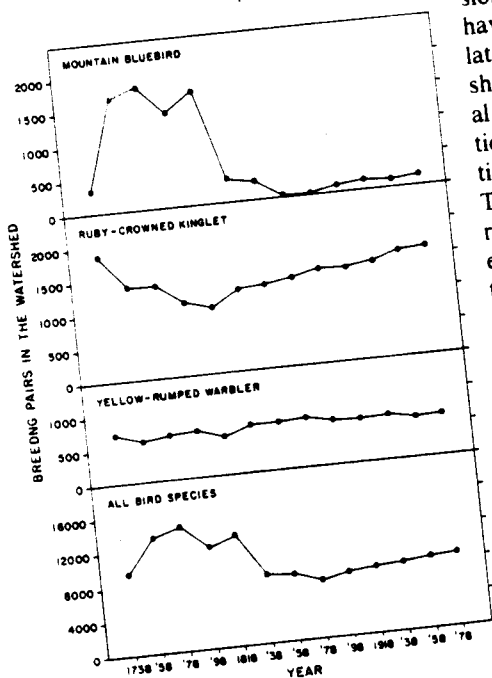


Figure 3. Estimated population sizes of breeding birds in upland forests of the Little Firehole River watershed, based on data from Taylor and Barmore (1980) and the trends shown in Figure 1. Populations in meadows and riparian forests, which cover approximately 16% of the watershed, are not included because appropriate population density data are not available for these habitats.

Table 1. Relative values of plant communities and successional stages for elk habitat in the Little Firehole River watershed.*

Table 1. Relative values of plant communities and their habitat in the Little Firehole River watershed.*						
Plant community type	Potential forage value	DISTANCE COEFFICIENT				
		DISTANCE (m) TO COVER OR WATER				
		0-320	320-800	800-1500	1500+	
Alluvial woodland adjacent to moist meadow	10	1.0	0.9	0.7	0.5	
Meadow	9	1.0	0.9	0.7	0.5	
Upland forest; early successional stages	7	1.0	0.9	0.7	0.5	
Upland forest; late successional stages	3	1.0	0.9	0.7	0.5	
Upland forest; middle successional stages	2	1.0	0.9	0.7	0.5	

*Based on models and discussions by Asherin 1973, Basile and Jensen 1971, Black et al. 1976, Hershey and Legee 1976, Lonner 1976, Lyon 1971, Marcum 1975, 1976, Pengelly 1963, Reynolds 1966, Stelfox et al. 1976, Thomas et al. 1976, and Winn 1976.

density. Nevertheless, the overall patterns are valid to the extent that they show the constraints of habitat on potential populations.

We were also able to consider the effect of landscape change on elk. Using a model much like that developed by Thomas et al. (1976), we examined changes in three critical habitat features during the last 200 years, namely, forage quantity and palatability, shelter (or cover), and water. The forage and shelter provided by an individual forest stand change greatly during postfire succession. Early successional stages usually have the best forage whereas middle and late successional stages provide the best shelter. However, because elk use several different kinds of habitat, the distribution and interspersed plant communities and successional stages is critical. Thus the center of a large meadow or recently burned area may receive little elk use, despite abundant forage, if it is too distant from shelter or water, and the potential shelter of very extensive tracts of mature forest may be largely ignored if little forage is available (Black et al. 1976, Hershey and Legee 1976, Marcum 1975, Reynolds 1966, Stelfox et al. 1976, Thomas et al. 1976, Winn 1976).

We developed a relative ranking system by which every type of plant community and successional stage in the Little Firehole River watershed was assigned a value from 0-10 to indicate potential forage value (Table 1). These values were subjective, based on published literature and our own observations in the study area. We then divided the watershed into 1429 units of 5 ha each, identified the dominant vegetation type within each unit, and assigned appropriate values to each. Every value was multiplied by a distance coefficient

reflecting the distance to the nearest shelter or water if those features were not present within the unit itself (Table 1), the product being our elk habitat index. In this manner we analyzed our reconstructed vegetation mosaics for 1778, 1878, and 1978.

Figure 4 (a, b, and c) shows the results for three 5-ha units having different histories of fire and forest regrowth. As a result of changes in stand structure, the quality of elk habitat has varied greatly. However, when we averaged the values for all 1429 individual 5-ha units to obtain an estimate of elk habitat quality for the watershed as a whole, we found much less difference among the landscapes of 1778, 1878, and 1978 (Figure 4d). There are probably two main reasons for this result. First, temporary increases in habitat quality in one part of the watershed (due primarily to the great improvement in forage after fire) have been balanced by decreases resulting from forest maturation on other areas burned earlier. Second, and probably more important, the best habitat is in and around moist meadows where forage, shelter, and water occur in close proximity. In fact, our model may underestimate the habitat quality of subalpine meadows in the park, since we reduced our elk habitat index in the centers of large meadows to reflect the distance to shelter. However, the shelter requirement apparently is much less critical for elk populations are not hunted by man, and elk in the park are frequently observed feeding in the centers of large meadows. We are unable to determine whether the fires in the surrounding uplands burned the meadows and adjacent

*L. Irwin, personal communication.

vial woodlands. We assumed that the fires in these areas were of low intensity and produced little change in community structure or elk habitat. Although our results suggest that fires may not greatly influence the overall quality of elk summer range on the high plateaus of Yellowstone, elk are attracted to recently burned areas (Davis 1977), and over much of the subalpine zone, moist meadows are less common than in the Little Firehole River watershed. Where meadows are less common, summer elk populations may fluctuate in response to changes in the upland landscape.

IMPLICATIONS FOR AQUATIC ECOSYSTEMS

One of the most interesting and attractive features of the park is Yellowstone Lake. This virtually unpolluted subalpine lake covers 354 km² and contains populations of the native cutthroat trout (*Salmo clarkii*). The trout support a complex food chain including pelicans, ospreys, otters, and bears. Some evidence indicates that the lake's net primary productivity has declined during the last century, as has its carrying capacity for trout and associated top predators (Shero 1977, US National Park Service 1975). Because the period of apparent decline coincides with attempts at fire control, some have suggested that the cause is reduced nutrient input to the lake due to biotic immobilization by forests. As noted earlier, however, our research indicates that the natural fire regime has not been greatly altered by

man's activities in the Yellowstone subalpine zone, particularly in the very remote areas that drain into Yellowstone Lake.

Rather than attribute the cause to fire suppression, we favor the hypothesis that lake productivity is to some extent synchronized with the long-term fire cycle that seems to prevail in the watershed of Yellowstone Lake. A variety of evidence supports this hypothesis. For example, experiments in the Rocky Mountains have shown that removal of mature forest from 40% of a subalpine watershed results in an increase in total water discharge of 25% or more (Leaf 1975). The increase is due to several factors related to the distribution and melting of the winter snowpack. Albin (1979) compared two small tributary streams of Yellowstone Lake; about 20% of one watershed was burned by fires 36 and 45 years previously, whereas the other watershed was unburned. The burned watershed had greater seasonal variation in streamflow and greater total water discharge per hectare. If a large portion of a subalpine watershed burns at intervals of approximately 300 years, as seems to occur in the Little Firehole River watershed, then streamflow also may exhibit a long-term cycle over and above yearly and seasonal fluctuations. During the high-discharge portion of the cycle, especially in years of high snowfall, debris is washed out of stream channels, new channels are cut, and new alluvial deposits are created. Such events influence habitat for fish as well as for floodplain species like willow and alder, which in

turn are important browse species for elk and other terrestrial animals (Houston 1973).

But more important to the question of Yellowstone Lake is the nutrient content of stream water. Immediately after deforestation by fire or cutting there often is an increase in dissolved minerals due to erosion, reduced plant uptake, increased microbial activity, increased leaching, and the release of elements from organic matter by fire (Bormann and Likens 1979, McColl and Grigal 1975, Wright 1976). The increase is usually short-lived, lasting several years at most (Albin 1979, Bormann and Likens 1979), but it may be important as a periodic nutrient subsidy (Odum et al. 1979) to oligotrophic aquatic ecosystems. As young forests become established, biotic immobilization is so effective that nutrient concentrations in stream water fall to very low levels (Bormann and Likens 1979, Marks and Bormann 1972, Vitousek and Reiners 1975). Thus a watershed dominated by early and middle forest successional stages (e.g., the Little Firehole River watershed during the 1800s) would produce relatively nutrient-poor water. As forests reach late successional stages, tree growth and net primary productivity decrease, nutrient uptake is less, and consequently the leachate is richer in dissolved minerals (Bormann and Likens 1979, Vitousek and Reiners 1975).⁴

Thus, although the possible connection between fire suppression and reduced productivity in Yellowstone Lake is plausible, an equally attractive alternative hypothesis is that extensive fires in the watershed about 100 years ago replaced many late successional forests with early successional stages. As young forests over much of the watershed began utilizing soil nutrients more efficiently, the total amount leached into stream water feeding the lake was reduced accordingly. If this is true, any recent decline in lake productivity may be a natural phenomenon that has occurred many times in the past and will be alleviated as forests in the watershed mature. Of course, the Yellowstone Lake watershed is very large (ca. 2600 km²), and landscape patterns over this large area may be in a state of dynamic equilibrium, or what Bormann and Likens (1979) have referred to as a shifting mosaic steady

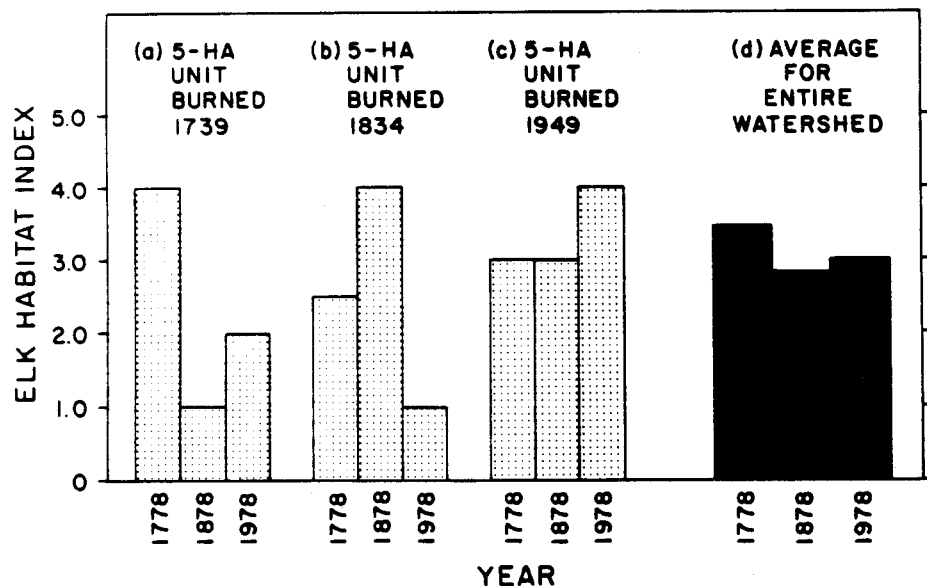


Figure 4. Elk habitat index (see text) for three representative 5-ha units and for the entire Little Firehole River watershed (d) in 1778, 1878, and 1978.

⁴Pearson, J. A., D. H. Knight, and T. J. Fahey. Unpublished ms. Net ecosystem production and nutrient accumulation during stand development in lodgepole pine forest, Wyoming.

state. If this is found to be true for the Yellowstone Lake watershed, then total nutrient input to the lake should be about the same from year to year (though the source would vary), and some other explanation for the decline in lake productivity will be required.

CONCLUSIONS

After a century of ecological research that focused largely on species or individual communities or ecosystems, there now is a growing interest in still higher levels of organization such as the landscape and biosphere. Changes in landscape patterns influence a variety of natural features including wildlife, water and nutrient flow, and the probability of different kinds of natural disturbances. Given a sufficiently large area and a natural disturbance regime, various measures of landscape pattern may remain fairly constant over time despite dramatic cyclic changes in localized areas such as a small watershed. Such "steady states" have been demonstrated or hypothesized for a Swedish boreal forest (Zachrisson 1977), high-elevation fir forests in New England and elsewhere (Sprugel 1976, Sprugel and Bormann 1981), primeval northern hardwood forests of North America (Bormann and Likens 1979), and mesic deciduous forests of the southern Appalachians (Shugart and West 1981). Our results suggest that strong cyclic changes occur on areas of at least 100 km² in Yellowstone National Park, but more research is needed to determine if the landscape patterns in the park as a whole are in a state of equilibrium. Large wilderness areas, when protected from pollutants and managed so that natural perturbations can continue, provide the best and probably the only locale for studying the kind of landscape changes that occurred for millennia in presettlement times.

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Fire Management in Yellowstone National Park

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THE NATURAL ENVIRONMENT OF YELLOWSTONE

YELLOWSTONE National Park, located in the extreme northwestern corner of the state of Wyoming, occupies an area of approximately 3,500 mi² (9,000 km²) and is the central portion of a vast mountainous, upland plateau astride the Continental Divide. Elevations in the park range from 5,000 to over 11,000 feet (1,500-3,400 m). The park is characterized by several broad, forested volcanic plateaus ranging in elevation from 7,000 to 9,000 feet (2,000-2,700 m). These plateaus are bordered by mountains on the north and east sides.

The climate of Yellowstone Park is characterized by long, cold winters; short, cool summers; and a resultant short growing season. Frost occurs most nights at higher elevations; at lower elevations nights are always cool. The average temperature at Lake, near the center of the park, during the month of July is 55.2°F (12.9°C) and for January is

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10.7°F (-11.8°C). Summer temperatures generally range from 40°F (4.4°C) at night into the 70's F (20's C) in the daytime. Mean annual precipitation ranges from 10 inches (254 mm) at Gardiner, Montana, to 70-80 inches (2,100-2,400 mm) along the Continental Divide in the southwest corner of the park (Dirks, 1974). Lightning occurs rather frequently during the summer. From 58 to 3 (mean=17) resultant fires have been recorded each year, from 1931 to 1974 normally during July and August.

About 80 percent of the park is forested. Lodgepole pine (*Pinus contorta* Dougl.) and spruce-fir (*Picea engelmannii* Parry-*Abies lasiocarpa* (Hook.) Nutt.) forest types predominate, followed by a smaller Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.) zone. Nonforest vegetation is widely interspersed throughout the forest areas. Extensive grassland and sagebrush areas occur along the lower river valleys. Mesic meadows are scattered throughout the forests on moist sites, along streams and around ponds. On the upper plateau levels and mountain slopes, sub-alpine meadows are found. The limited areas above 10,000 feet (3,000 m) support an alpine tundra (Despain 1973).

MANAGEMENT CONCEPTS

Over 1,900,000 acres (770,000 ha) of Yellowstone Park are managed as wilderness. The administrative policy for the management of natural areas of the National Park system such as Yellowstone clearly stated in 1970 "The presence or absence of natural fire within a given habitat is recognized as one of the ecological factors contributing to the perpetuation of plants and animals native to that habitat. Fires in vegetation resulting from natural causes are recognized as natural phenomena and may be allowed to run their course when such burning will contribute to the accomplishment of approved vegetation and/or wildlife management objectives" (U.S.D.I. National Park Service, 1970). Such a program was initiated in Yellowstone in 1972. This paper describes the implementation and 3 years results of this concept. Research procedures implemented are also described.

BIOLOGICAL RATIONALE TO ALLOW NATURAL FIRES

Fire is a natural part of the environment that originally shaped the post Pleistocene ecosystems of Yellowstone National Park. One only has to fly over Yellowstone slowly a few times to realize what an influence fire has had in shaping this landscape. Evidence of fire is everywhere. Baker (1969) found evidence of fire beginning more than 5,000 years ago. A number of species are adapted to fire. The serotinous cones of lodgepole pines, the thick bark of Douglas-fir, and root sprouting by rabbit brush, aspen, and other species are examples. The structure and composition of some plant communities are dependent on fire, as exemplified by dense lodgepole pine and Douglas-fir stands. Fire maintains forest-grassland boundaries and maintains a natural diversity in a landscape of otherwise uniform environment. Fire creates pioneer habitat and greatly affects the rates of mineral cycling and flow.

The extent to which natural fires are controlled determines the degree of departure from natural conditions. With suppression, changes occur in the structure and composition of many plant communities and their interaction with other segments of the biota. Forest boundaries advance, fire-susceptible species gain an unnatural prominence, and climax communities develop over unnaturally large areas. Insect and disease organisms may obtain an unbalanced advantage, creating an overabundance of litter and deadfall. This in turn changes mineral pool relationships in the undecomposed organic matter, changing soil composition. Faunal relationships may also be expected to show departures from normal, since many species of birds and mammals are adapted to plant communities that develop following fires (Despain, 1972).

Fire control action itself produces unnatural effects, including scars of fire lines, the fertilizing effect of modern retardants, and leaving unburned many acres that would otherwise have burned. Any re-vegetation or rehabilitation programs are also unnatural.

Two research projects have aided in understanding Yellowstone's fire ecology. Studies on succession in lodgepole pine communities carried out by Taylor (1973) begun in 1965 have indicated what can

be expected in the lodgepole pine zones. He showed a 3-fold increase in species of plants, birds and small mammals in lodgepole pine stands burned 25 years earlier. Houston (1973) dated fires as early as 1525 on the northern Douglas-fir-steppe zone of the park. Historically this zone has the highest natural fire frequency in the park. Lightning fires have been suppressed in the past 80 years. This area should probably have burned over between one and four times since the establishment of the park in 1872. These two studies helped give us confidence that no permanent damage would result in allowing fires to burn, indeed fire suppression was causing departure from natural conditions.

THE NATURAL FIRE PLAN

In the spring of 1972 a new approach to fires in natural areas was instituted to allow naturally-occurring fires to run their course over some 340,000 acres (138,000 ha) of Yellowstone Park.

The area considered for allowing naturally ignited fires to run their course met the following criteria:

1. The area should be managed as wilderness.
2. Natural fires occurring in the areas must not pose an immediate threat to primary visitor-use areas such as Old Faithful.
3. Human life must not be endangered under any circumstances.
4. Lands under the management of other agencies must be protected.

The following steps were taken to fit the proposed program into the above criteria:

1. We established a characteristic behavior pattern for fires in the park from detailed records kept from 1931 to 1971. A history of project fires in the park indicated that the dominant direction of travel was to the northeast and wind was necessary for large fires to develop.

2. Areas were then selected which were east or northeast of visitor use areas. Here, under nearly all conditions, lightning-caused fires would be allowed to burn. The areas most suitable lay on the Mirror Plateau in the northeast quadrant and on the Two Ocean Plateau in the southeast quadrant. Selection of as large an area as possible was

made, using natural barriers as boundaries within these plateau areas. With the aid of maps, aerial photos, and on-the-ground surveys this was accomplished and the two areas were delineated. The northern Mirror Unit consists of approximately 191,000 acres (77,000 ha) of lodgepole pine and spruce-fir forest interspersed with open meadows and steppes lying between the Yellowstone River on the west and the Lamar River drainage on the east. The southern Two Ocean Unit includes approximately 150,000 acres (61,000 ha) of spruce-fir, lodgepole, and open meadows lying between Heart Lake on the west and the Yellowstone River on the east (Fig. 1).

3. We then analyzed the fire history of the past decade in these two areas. In 1971, four lightning fires were suppressed in this area during rather severe burning conditions. Acreage burned was negligible. By projecting these same fires through subsequently known weather conditions and burning indices, we determined that all would have probably gone out with a combined maximum acreage of about 1,000 acres (429 ha) and a minimum acreage of around 100 acres (51 ha).

One suppressed fire on the Two Ocean Unit may have consumed a maximum of 700 acres (283 ha) and a minimum of 100 acres (53 ha) had no suppression action been taken. In addition, we projected the behavior of 13 lightning fires in the Two Ocean Unit on which full suppression activity had been taken in the years 1960-69. Maximum acreage that these combined fires may have burned was estimated at about 5,000 acres (2,200 ha) and a minimum of 700 acres (283 ha) before they would have been extinguished by natural conditions.

4. The above projections, in spite of an imperfect knowledge of fire behavior, enabled us to come up with a rather subjective hypothesis that naturally-caused fires, at least in these areas of Yellowstone National Park, would have plenty of room to run their course even during periods of extreme burning conditions that exist mainly during July and August, and would extinguish themselves as naturally as they began, without endangering human life or property.

5. Much of the rest of the park was designated as conditional zones. Late in the fire season, when fall snow storms are common enough to extinguish fires before they attain large size, lightning-caused fires would be allowed to burn at the option of the superintendent and advisors.

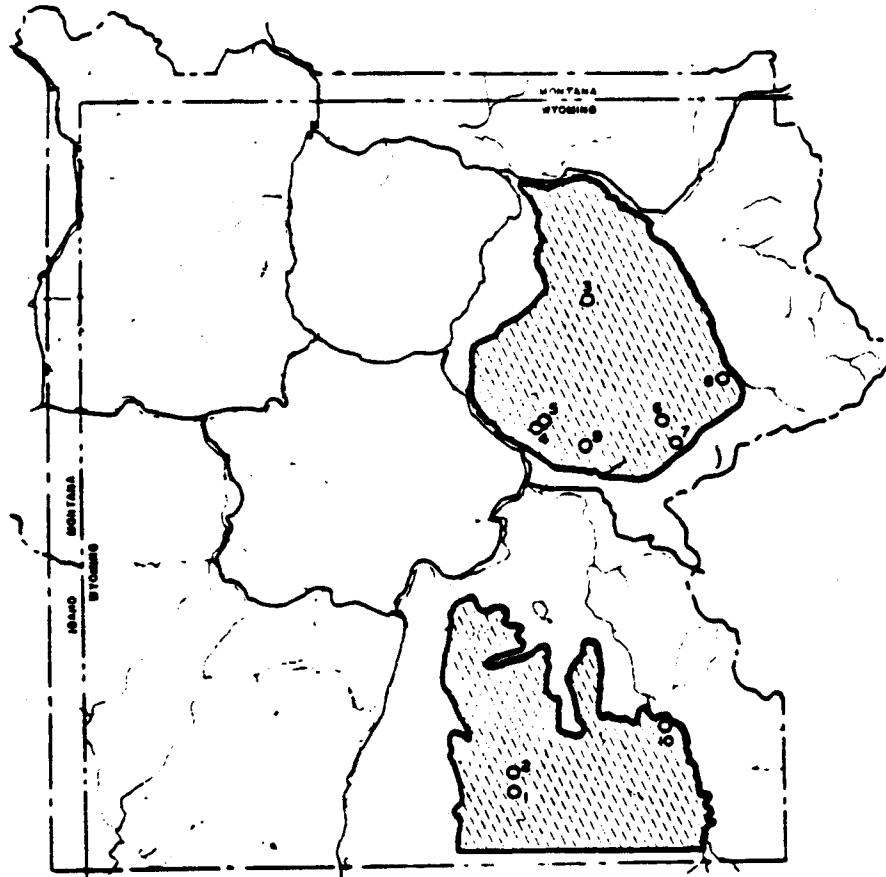


Fig. 1. Yellowstone National Park showing location of Natural Fire Zones and natural fires 1972-1974. 1=Two Ocean-1, 2=Two Ocean-2, 3=Wrong Creek, 4=Cottongrass Creek, 5=Bluff Creek, 6=Raven Creek, 7=Mist Creek, 8=Willow Creek, 9=Stonetop, 10=Trail Creek.

We then set about to test this hypothesis with our natural fire plan for these two areas. In 1972, the first year of the plan, we took suppression action on nine lightning fires in the park outside the fire management units. Two fires in the Two Ocean Unit were ignited by lightning on August 11th. Monitoring of these fires began on the day of ignition. Both went out within 2 days and burned little area. One

burned a few rotten logs left from a 1931 fire and the other one burned at the base of two spruce trees (Table 1).

In 1973 we took suppression action on 23 lightning fires which included two fires of project proportions (greater than 10 acres, 4 ha) outside the units. One lightning fire occurred on the Mirror Unit. This small fire was monitored for its duration of 2 days (Table 1).

In 1974 the plan, with its accompanying hypothesis, was put to its most severe test. Precipitation in June was 34 percent of normal and by July 14th we had extreme burning conditions. July continued unusually hot and dry and 16 lightning fires outside the natural fire zones were suppressed during the month. One of these was the Fan Creek fire which consumed 470 acres (190 ha) and cost over \$450,000 to suppress. On July 2nd lightning ignited a fire on the Mirror Unit. It was monitored for 2 days and was out at the end of the second day.

Toward the end of July, four lightning fires appeared on the Mirror Unit. These were all monitored. One went out at a small size but three of them—Raven Creek, Bluff Creek, and Willow Creek—became very active on July 26th when a dry cold front passed through the area. Willow Creek had not been detected until that time. These fires burned very intensely through July 28th and would have required considerable effort and expense to suppress. After the cold front had passed the Stonetop fire ignited, burned a small area and went out (Table 1).

Precipitation in August was 131 percent of normal and mean monthly temperature was 2.5°F (1.4°C) below normal at Lake. All the fires but Willow Creek went out during this period. Willow Creek smoldered in areas of deep duff accumulations and became active again in September which had only 15 percent normal precipitation.

On September 16th a lightning fire was discovered on the Two Ocean Unit in the vicinity of Trail Creek. The first day after discovery it consumed 5 acres (2 ha) of sedge meadow and secured a good enough foothold in some bordering spruce-fir to move slowly southwesterly to cover an area of about 36 acres (15 ha) by October 2nd. Winds were light from the northwest during this period. On the afternoon of October 2nd a local cold front passed through the area and carried this fire northeasterly across the Yellowstone River. Its size at 1700 on October 2nd was about 550 acres (223 ha). On Octo-

Table 1. Natural fires allowed to burn in Yellowstone National Park, 1972-1974.

Named Fire	Duration	Slope	Aspect	Elevations		Vegetation Type	Areas Burned
				Feet	Meter		
Two Ocean - 1	8/11-8/13/72	—	SW	8000	2620	1931 burn in shrub slope	420 ft ² (39 m ²)
Two Ocean - 2	8/11-8/13/72	flat	NW	8400	2560	spruce-fir	110 ft ² (10 m ²)
Wrong Creek	7/12-7/15/73	5%	NE	8400	2560	spruce-fir	222 ft ² (21 m ²)
Callongrass Creek	7/0-7/8/74	5-10%	SW	8000	2620	climax lodgepole	0.7 a (28 ha)
Bluff Creek	7/23-8/14/74	30%	NE	8200	2500	lodgepole ^b and spruce-fir	50 a (20 ha)
Raven Creek	7/23-8/27/74	30%	SW	8400	2560	spruce-fir	35 a (14 ha)
Mist Creek	7/23-7/24/74	—	NW	8400	2560	spruce-fir	36 ft ² (3.4 m ²) ^a
Willow Creek	7/23-10/10/74	50%	NE	8400	2560	spruce-fir	160 a (65 ha)
Stonctop	7/28-8/10/74	20%	E	8700	2850	whitebarked pine	0.2 a (0.1 ha)
Trail Creek	9/10-11/10/74	flat	flat	7800	2380	spruce-fir lodgepole ^b sedge meadow	580 a (235 ha)

^a Observed from helicopter only, area is ocular estimate only.^b Successional lodgepole pine, about 250 years old, with spruce and fir reproduction in the understory.

ber 24th flames were still visible within the burn, but by November 10th snowfall had extinguished it (Table 1). Size increase during this period was negligible.

The summer of 1974 provided us with perhaps some of the most severe burning conditions of the past 10 years. We had ignition and hot, running fires in many of the fuel types and slope aspects typical of the park. We consider the program so far to be entirely successful. Based on past fire history and the results of this new management program we have drawn a few preliminary conclusions which we feel are valid for normal and drier than normal fire seasons such as the one just completed. Some of these preliminary conclusions are listed as follows:

1. We always have lightning occurrences and some fires result.
2. There is a very low percentage of fires ignited compared to the number of lightning strikes to the ground.
3. There is a 100 percent chance that a lightning fire will occur in either of the two management units.
4. Unique environmental conditions must occur at the time of ignition to allow the fire to continue. These conditions most often include low fuel moisture (6-10 percent), high temperatures (80°F or 27°C), low humidities (20 percent), or wind at 20 mph (32 kmph) or more.
5. Fires originating in lodgepole pine forest must reach the canopy or they remain inactive and probably go out with the next high humidity day. They run through the canopies rapidly when exposed to winds.
6. Most lightning fires originate in spruce-fir. The "sleeper" fire (one that exists for a few days before being detected) almost always can be traced to a clump of spruce-fir.
7. Fires originating in spruce-fir stands have a better chance of carrying through high humidities and calm days, even periods of rain and snow. These make dramatic runs with hot, dry winds. Winds do not have to reach the velocities that they do in lodgepole.
8. Winds occur for short periods in the afternoons and those that moved these fires were mainly caused by local cold fronts or thunderstorms. Winds of the velocity to cause fires to reach appreciable acreages occur sporadically from 8 to 10 times during the short, normal

fire season of July and August. When they do occur they are usually of short duration, lasting only a few hours.

9. Fires are most active during the hours of 1300-1700. Nights are almost always cool enough to keep fires on the ground until afternoon.

10. Fires reach their maximum acreage in spectacular fashion in a very short period of time when the wind is blowing. Between these short periods they remain on the ground and quite stationary.

11. For every day of extreme burning conditions, which include high wind, we have at least one counteracting day of wet, rainy or snowy conditions during the normal fire season at our elevations. However, extended dry periods may occur.

12. Large acreages will not burn every year. On those years when conditions are right, fires could probably be seen somewhere in the park from late spring to late fall. Both Willow Creek and Trail Creek survived some extended wet cold periods. Fires of more than 1,000 acres (400 ha) are rare and very few fires exceeded 50,000 acres (20,000 ha) in the past.

These conclusions will be further tested. The program has opened up a whole new line of thinking and opportunity for research, which hopefully will allow for future expansion of the role of natural fire in all wilderness areas of Yellowstone National Park.

RESEARCH PROCEDURES

Concurrent with the management policy of allowing naturally-caused fires to burn within defined limits a research program was implemented. The purpose of this research is to investigate the behavior of these fires and subsequent ecological changes. The data obtained will aid in understanding the role of fire in Yellowstone ecosystems and also provide better information to help predict fire behavior under given circumstances. These data will be needed to protect developments when this fire management policy is applied to other areas of the park. It will also aid in defining conditions under which fires will be allowed to burn in conditional natural fire areas.

INITIAL PHASE STUDY

When a fire in one of the two natural fire management units is re-

ported it is photographed from the air as soon as possible and video tapes made. This aerial surveillance is maintained intermittently throughout the life of the fire. Two men are dispatched by helicopter with the initial phase study kit—including a belt weather kit, a hygrothermograph, fuel stick and scales, camera and film, and other instruments as needed. Their responsibilities include recording cause, initial burning conditions, behavior of the fire, and initiating hourly weather readings.

A Fire Boss is assigned to coordinate ground action. He will supervise all personnel for safety reasons.

As soon as possible a fuel moisture stick is set up and weighed. Other fuel moisture stick stations are established if deemed necessary and feasible during the course of the fire.

DURING A GROWING FIRE

When it becomes evident that a fire is going to burn at least 40-50 acres (17-20 ha), a time lapse camera is installed to view the fire from a distance. Time interval of one minute is set. Some 15 X 25 meters permanent plots are also set out in representative communities to measure the effects of burning on the vegetation.

The corners are located and two corners diagonally across the plot are marked with steel fence posts. The plots are 15 X 25 meters with the long axis oriented parallel with the slopes, or perpendicular to the advancing front if there is little or no slope.

A priority of information to be gathered is necessary. Measurements are performed in a special sequence and as many of the measurements are taken as time allows:

1. Fuel load estimates are made. The method used is that developed by the Northern Fire Research Lab at Missoula (Brown, 1974). The lines where intercepts are tallied follow the deliniation lines of the plot. Ten lines are thus obtained each up to 10 meters in length.
2. Samples of dead fuel of the several size classes are collected in tin sample cans for moisture content determination.
3. Samples of living plant material from the needles and branches of the different tree species, leaf and twig samples from shrub, and whole plant samples from the major herb species are collected to be analyzed for both moisture content and mineral content. These are

placed in tin sample cans and weighed at a later date. Samples from each major species are taken during this step.

4. Soil samples are taken with a soil tube. Approximately 100 grams from each horizon is placed in tin sample cans.

5. Photographs are taken from each steel corner post facing toward the plot.

6. Vertical photographs are taken of each of 10 herb plots with a support (Fig. 2) that photographs a 1 meter by 1 meter area with an instamatic camera. This support is placed at 5 meter intervals along a line 5 meters from each long side of the plot. Each of these plots is marked with large nails.

7. The dbh of the trees is tallied by 5 meter wide segments according to species.

8. Shrub crown cover is determined by the line transect method along one line 5 meters from the edge. This is the same line along which the herb plots are established. That portion of the tape covered by a vertical extension of the crown to the tape is tallied to the decimeter.

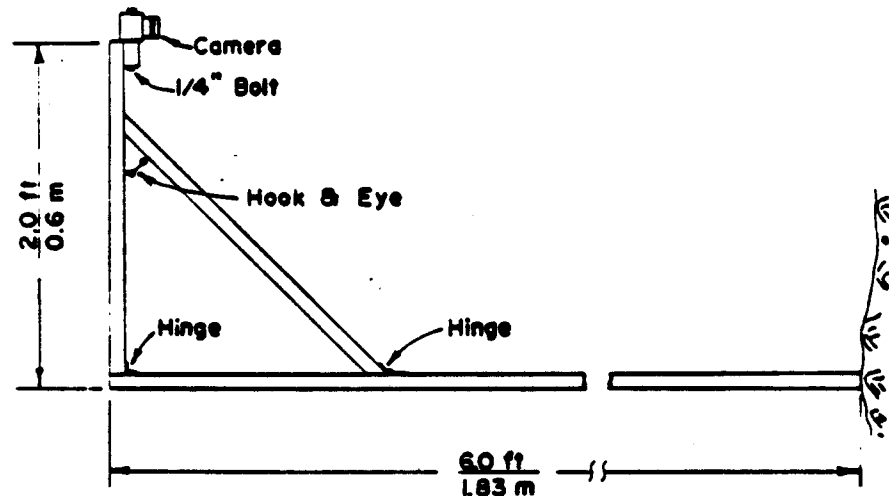


Fig. 2. Vertical platform for the photography of 1 m² of ground surface constructed of standard 1 X 2 inch (2 X 5 cm) pine. A Kodak instamatic camera was used. other cameras may require different vertical distances.

9. A species list and cover class estimate is compiled. The following cover class designations are used: P=1, 1=1%-5%, 2=5%-25%, 3=25%-50%, 4=50%-75%, 5=75%-95%, 6=95%-100%, (Daubenmire, 1959).

10. Water can heat integrators (Beaufait, 1966) are positioned within the plot to represent the different types of fuel accumulations. Tempilaq is used to measure duff and soil temperatures (Fenner and Bentley, 1960).

11. A survey of the plot is made for animal signs. Pellet groups, nests, burrows, cone caches, etc., are identified and located by coordinate system along sides of plot.

12. Voucher specimens of all living plant species are collected whether in flower or not. This includes mosses and lichens.

13. Surface water samples are taken from streams and lakes that are likely to be burned over. This information will provide base line data.

POSTFIRE FOLLOWUP

Followup over a several year period is essential in this project. The photopoints will be rephotographed yearly for 5 years, then on a 5-year schedule until change is slow enough to warrant a longer interval. The herb plots will be rephotographed at similar intervals.

Remeasurement of quantitative parameters on a periodic schedule will be followed to keep track of the quantitative changes in species diversity and biomass.

These methods were implemented this past fire season (1974) and found generally to be quite workable. Two men can set up a permanent plot in about 3 hours. Uncertainty as to the future activity of the fire caused problems in determining sample plot location. Five plots were set up but only one burned. There was only one period of active burning on most of the fires and during that time it is impossible to set up a plot and insure the safety of the researchers. If August had been more typical the fires probably would have burned the other plots.

Because the fire did not burn the permanent plots previously set up some permanent transects or plots will be set up in the areas that

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burned. These will be followed through succeeding years the same as outlined for the other plots.

The timelapse cameras were very useful. They allowed us to observe the activity of the fire in compressed time as well as see what happened when no observers were on the fire. The one minute interval with the camera shut off at night gives about 6 days on a 50-foot roll of film.

We hope that information gained this season will allow us to expand the natural fire concept to other areas within the park and thus allow more area to be managed as a more nearly natural landscape.

ACKNOWLEDGMENTS

This program would not have been instituted if it had not been for the efforts of many people. We thank Superintendant Jack Anderson who had courage enough to allow a potentially controversial approach to fire, Bill Hendrickson and others who laid much of the ground work, and Ted Bucknall who helped to formulate the present fire management plan. We also thank the numerous unnamed technicians and aids that kept and preserved records of both present and past fires.

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WILDFIRES IN NORTHERN YELLOWSTONE NATIONAL PARK¹

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Abstract. A sample of 40 fire-scarred trees was used to reconstruct the frequency and size of fires during the past 300–400 years in northern Yellowstone National Park. Best estimates of frequency suggested mean intervals of about 20–25 years between fires, after adjustments had been made for the recent influence of modern man. Agreement in fire dates over wide areas suggested the occurrence of 8 or 10 extensive fires in the past 300–400 years. Euro-American man has substantially reduced the natural fire frequency for about 80 years and has thus contributed to changes in plant succession.

INTRODUCTION

A comparison of historic with recent photos of northern Yellowstone National Park suggested the hypothesis that natural fires had been a major influence on plant succession (Fig. 1). The changes in vegetation have occurred on the "northern winter range" of the park, an area that supports a unique assemblage of native ungulates with their complement of predators and scavengers (Houston 1971a). Data on frequency and size of past fires were considered necessary to understand trends in plant succession and, eventually, the relations between ungulates and their habitats. The objective of Yellowstone Park, as a natural area, is to maintain representative ecosystems in as near pristine conditions as possible (Houston 1971b). Therefore an important purpose in this study was to assess the effects of attempting to suppress natural fires nearly since establishment of the park in 1872.

THE STUDY AREA

The 81,000 ha study area extends down the elevational gradients of the Yellowstone, Lamar, and Gardner rivers from about 2,600–1,500 m (Fig. 2). U.S. Department of Commerce Weather Bureau records (1960) for Mammoth Hot Springs at 1,900 m showed a 30-year (1930–59) mean annual precipitation of 39.49 cm. Precipitation on most of the area ranges 30–45 cm. Records show a mean annual temperature of 7.8°C; July, as the warmest month, averaged 30.8°C; January, as the coldest, –14.0°C. Reviews of historical records and of dendroclimatology data show that the area has been subjected to wide variations in precipitation, and periodic droughts have been common. Prevailing surface winds, an important consideration in interpreting fire data, are usually from the southwest but are often changed to west by the topography of the study area.

The vegetation of the area is primarily a steppe with interspersions of conifers occurring as single



FIG. 1. Tower Junction, Yellowstone National Park. Upper photo by J. P. Iddings ca. 1885 (U.S. Geol. Survey No. 152); lower, D. B. Houston, 1970. The increase of *Artemisia tridentata* on bunchgrass steppes (in this case *Festuca idahoensis*), the increase in area and density of coniferous forest (*Pseudotsuga menziesii*), and the decline in aspen typify vegetative changes on the study area.

isolated trees or small stands at lower elevations, and as more continuous forests at higher elevations or on north slopes. The "mesic meadows" in valley bottoms are characterized by *Deschampsia* spp. and *Carex* spp. Bunchgrass steppes on upland slopes are characterized by *Agropyron spicatum*, *Festuca idahoensis*, *Koeleria cristata*, *Stipa* spp., and *Poa* spp.

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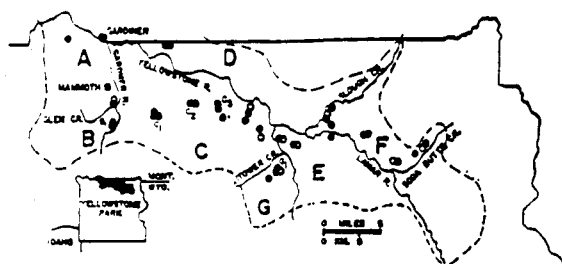


FIG. 2. The northern Yellowstone Park study area showing sample units and locations of live cut (●) and dead (○) fire-scarred trees. Specific stands referred to in text are designated by unit subscripts.

in various combinations. Important shrub components on bunchgrass steppes include *Artemisia tridentata*, *Chrysothamnus nauseosus*, and *C. viscidiflorus*. *Pseudotsuga menziesii* (Douglas-fir) and *Pinus contorta* (lodgepole pine) characterize the most abundant forest types, and may occur in either pure or mixed stands. *Abies lasiocarpa* (subalpine fir) and *Picea engelmannii* (Engelmann spruce) are locally abundant in pure or mixed stands on mesic north slopes and in riparian situations. Small stands of *Populus tremuloides* (aspen), *Pinus flexilis* (limber pine), *Juniperus scopulorum* (Rocky Mountain juniper) also occur on the area. Physical evidence for past fires is abundant as charred living trees showing multiple fire scars (mostly Douglas-fir), charred remains of trees, and fragments of charcoal in the soil.

METHODS

Presumed fire scars were pennant shaped and extended from the soil surface for several meters up the trunk (Weaver and Clements 1938, Molnor and McMinn 1960). I sampled scarred trees from areas known to have burned in 1870, 1886, and 1949. Results confirmed that scars resulted from fires, but showed that the actual year of the fire could be in error by at least ± 2 years because resin deposits, insect damage, and decay obscured some scars and made the choice of the fire annulus rather arbitrary. Unrecognized "false" or absent annuli may also preclude determinations of exact fire dates (Ferguson 1968). Whenever possible, I took samples from locations where outwardly similar patterns of scarring occurred on surrounding trees, in order to minimize the possibilities of sampling very small fires.

Preliminary attempts to sample fire scars by taking increment cores proved futile because of the complexity of the pattern of scars and the interior decay of many older trees. The information to be obtained was judged of sufficient importance to justify felling a small sample of scarred trees. Thirty-one living trees (29 Douglas-fir, 2 lodgepole pine) were felled at intervals of about 3–7 km on the study area (Fig.

TABLE 1. Average mean intervals between fires for 34 sampled trees

Unit	No. trees	Age of trees	No. scars	Fire interval (years)	Adjusted interval ¹
A	3 (1) ²	258 (164–306) ³	3 (2–4)	87 (77–101)	53
B	2	261 (205–317)	3 (2–4)	96 (90–102)	62
C	12 (2)	356 (264–465)	7 (4–9)	54 (36–88)	44
D	2	334 (325–344)	4 (3–5)	88 (69–108)	70
E	5 (2)	347 (286–406)	6 (4–7)	63 (49–101)	56
F	6 (2)	365 (125–485)	5 (2–8)	69 (59–81)	50
G	4 (1)	200 (146–254)	4 (3–5)	53 (37–69)	32

¹80-year adjustment, live trees only—see text.

²(No. dead trees)

³(range)

2), and cross sections removed from the bases of the trees. Nine fallen dead Douglas-fir showing multiple scars were also sampled. Sections were removed to a lab, dried, sanded, and examined with a 10× lens. The study area was subdivided into seven units because of differences in elevations and the possibility that physiographic features, such as major rivers with associated barren cliffs, may have been important natural fire breaks. Contiguous units CEF were sampled most intensively and are considered to be representative of much of the area.

RESULTS

Fire frequency

I used two different calculations of fire frequency. In the first the mean interval between fires on an individual tree was determined by dividing the age of the tree (Y) by the number of fire scars (S). An average mean interval between fires on individual trees was determined using

$$\bar{x} = \frac{\sum (Y/S)}{N_t}$$

where N_t is the total number of trees sampled on the unit. This approach has the disadvantage of saying little about variation in intervals; however, this is considered in the second calculation. A sample of 34 trees cut as isolated individuals in the steppe or from forest-steppe ecotones were used to infer a fire frequency for the steppe. Attempts to extend the fire chronology farther back in time by matching scars and rings on living with dead trees failed because of the complexity of the scarring pattern and the lack of indentifiable ring sequences. Wilcoxon rank sum tests ($P < .05$) showed no significant difference in frequency between live cut and dead trees, and these were combined (Table 1).

The 34 trees averaged 322 years of age, with 8 being older than 400 years. Average mean intervals between fires was 53–96 years. Mean intervals for individual trees was 36–108 years. Means for the major contiguous study units (CEF) ranged from

TABLE 2. Intrastand fire frequency

Stand	No. trees	Interval compared	Total no. scars for period	No. different fires ¹	Interval between fires			Adjusted interval -80 yrs.
					$\bar{x}$	Min.	Max. ²	
B ₁	2	1776-1970	5 (3, 2) ³	5	41	18	38	25
C ₁	3	1603-1970	19 (8, 4, 7)	16	22	6	40	17
C ₂	2	1693-1970	11 (7, 4)	10	28	7	45	20
C ₃	2	1706-1970	9 (5, 4)	6	44	6	53	26
D ₁	2	1646-1970	8 (5, 3)	6	54	14	60	41
G ₁	2	1773-1970	8 (5, 3)	6	33	6	44	20

¹ ± 2 years allowed for agreement on fire dates.² Excludes the interval from 1970 to most recent scar (see text).³ (No. of scars per tree)

54 to 69 years. Smaller samples from higher elevation (2,200-2,300 m) sites (BG) showed intervals of 53 and 96 years. The two trees from unit D were sampled above a series of natural fire breaks and supplemental increment coring from other portions of the unit showed that the interval of 88 years underestimated fire frequency. The interval of 87 years for unit A probably underestimates frequency because of a lack of suitable trees. The unit extends about 1,500-1,800 m at the lower limit of tree distribution; most trees occurred on riparian sites, on rock outcrops, and on talus slopes, which were poor locations to sample fire frequency. Additionally, many larger trees had been felled in this unit for construction and fuel during the early decades of the park. Part of unit A was added to the park in 1932, also after most of the larger trees had been felled.

Periods of 80 years were subtracted from ages of living trees and "adjusted" mean intervals calculated (Table 1) to assess fire frequencies prior to the suppression activities of modern man (discussed below). Mean intervals were reduced and became 44, 56, and 50 years in units CEF, respectively. Six trees in units CEF had obviously incomplete records, with sections of 50-150 years burned away by subsequent fires, with the result that adjusted intervals still probably underestimated the true frequency.

Two or three scarred trees were felled at intervals of 5-25 m along forest steppe ecotones in each of five stands, and fire dates were compared to give a second measure of frequency and to evaluate the completeness of records obtained from individual trees. Cross-dating of fire scars (allowing ± 2 years for agreement on dates) eliminated duplicate fires for intervals from 1970 to the pith date of the youngest tree, and reduced the calculated interval between fires (Table 2). The three trees of stand C₁ were cut within a few meters of one another, and showed 16 different fires between 1613 and 1970 with a mean interval of 22 years. Although similar fire dates occurred among the three trees, a date common to all three was not found. This indicated either that the

record for any one tree underestimated the frequency of fires to which the area had been subjected (because not all trees were scarred by every fire, or else scars were burned away by subsequent fires) or that, despite precautions in sampling, the record reflected many small fires. There appears to be no unequivocal means for separating these possibilities, but the correspondence in fire dates over wide areas and the obvious incompleteness of the records on some trees as a result of subsequent burning argue for the first possibility. Mean adjusted intervals of 20-25 years between fires were calculated by subtracting 80 years from tree ages and are considered to be the best estimate of the true fire frequency (Table 2). Substantial variation occurred in the intervals between fires, and minimum intervals were generally 6-7 years. In all cases the maximum intervals occurred from 1970 to the most recent scar (70-150 years) but this was considered not to be a valid measure because of the influence of modern man. The next largest interval between fires was 40-60 years in the five stands. It should again be noted that the two trees from unit D underestimated frequency for the overall unit because of their location.

Fire size

A determination of the size of individual fires was complicated by the discontinuous nature of the forest vegetation on the study area. However, some inferences were made by comparing fire dates on 22 trees in 18 different stands on units CEF (Table 3) with ± 2 years again allowed for correspondence on actual dates. This sample included the 17 living trees used in the analysis of fire frequency, plus five others cut from mesic riparian sites. Eleven trees from seven different stands within unit C showed 28 different fires from 1525 to 1870, with 17 fire dates occurring in more than one stand. Agreement in dates was directly related to sample size, and declined with the smaller number of trees from the two other units. Undoubtedly agreement could be increased by felling a larger number of trees, but this was neither possible nor desirable in the park.

TABLE 3. Intra and interunit comparisons of fire dates

Periods	Units			Possible large fires
	C	E	F	
	11 trees, 7 stands	3 trees, 3 stands	8 trees, 8 stands	
1500-1599 (5) ²	1525(1, 1) ¹ 1565(1, 1) 1583(4, 3)		1551(1, 1) 1583(1, 1) 1594(1, 1)	?
1600-1699 (13)	1609(1, 1) 1614(2, 2) 1635(2, 1) 1641(1, 1) 1667(1, 1)	1651(1, 1) 1672(1, 1)	1616(1, 1) 1627(2, 2) 1671(2, 2)	
1700-1799 (15)	1685(3, 3) 1691(2, 2) 1703(3, 3) 1715(3, 3) 1720(2, 2) 1728(2, 2) 1738(2, 2) 1748(2, 2) 1758(3, 4) 1763(3, 2)	1703(1, 1) 1715(2, 2) 1738(1, 1) 1768(1, 1)	1690(1, 1) 1703(3, 3) 1715(1, 1) 1738(1, 1) 1758(2, 2) 1766(1, 1) 1770(1, 1) 1776(3, 3) 1785(2, 2)	* ? *
1800-1899 (13)	1770(1, 1) 1776(4, 3) 1785(3, 3) 1790(1, 1) 1803(4, 3) 1811(1, 1) 1830(1, 1) 1856(6, 4) 1861(1, 1) 1870(5, 4)	1776(1, 1) 1785(1, 1) 1803(2, 2) 1856(2, 2) 1870(2, 2) 1892(1, 1)	1803(2, 2) 1811(1, 1) 1824(1, 1) 1848(1, 1) 1863(1, 1) 1870(2, 2) 1876(1, 1) 1893(1, 1)	* *
1900-1970 (0)				

¹(number of trees showing scar, number of stands)²Number of different fires allowing ± 2 years for agreement on dates.

Eight fire dates from about 1703 to 1870 occurred in six or more different stands in at least two of the three units (Table 3). Two other fires in or about 1583 and 1738 occurred in four different stands. In three other cases similar dates occurred on single trees at extreme ends of the sampled areas, but the lack of dates in intervening areas and the topography suggested that these most likely represented separate smaller fires. The occurrence of similar fire dates over wide areas suggested 8 or perhaps 10 extensive fires in the past 300-400 years. Additional support for the interpretation of extensive fires exists for the 1870 date. On August 26, 1870, Doane (Bonney and

TABLE 4. Lightning-caused fires on the study area 1931-71

Period	No. fires and ha burned			Years with	
	<0.10	0.11-3.9	>4.0	No fires	4 or more fires
1931-39	13	2		2	2
1940-49	16	3	1	3	4
1950-59	28	1		3	2
1960-69	17	7		1	3
1970-71	8	2	1	0	2
	82	15	2	9	13

Bonney 1970) described the general area of unit C as being "... about 30 miles in extent, with a general declivity to the northward. Its surface is an undulating prairie dotted with groves of pine and aspen." He goes on to say that "The great plateau had been recently burned off to drive away the game, and the woods were still on fire in every direction."

Only five fire dates were recorded from 1525 to 1599. This was to be expected because 400 years approaches the maximum life expectancy of Douglas-fir in this area (Fowells 1965), and comparatively few old scarred trees were available to sample. An abrupt decline in fire scars occurred shortly after establishment of the park, with only two dates in units CEF recorded for the 1890's, and none for the 20th century. Origin and characteristics of the fires that left scars in or about 1892 and 1893 could not be determined.

Ignition sources and fire suppression

Records show that suppression action was taken on 99 lightning-caused fires on the study area 1931-71 (Table 4). Fires occurred in 78% of these 41 years; 4 or more fires were reported on 32%, with 6 reported in each of 1936, 1949, and 1966; 7 in 1953 and 1971; and 11 during 1958. Over 80% of the fires were suppressed before reaching 0.10 ha in size, with the three largest reported at 65 ha in 1939, 735 ha in 1949, and 19 ha in 1971. In addition to fires that originated on the area, an additional 39 lightning fires were suppressed within 7 km of the south and west perimeters during the same period, some of which might otherwise have burned onto the area because of the prevailing winds. These records, of comparatively short duration, show that lightning is potentially a major source of natural fires on the area and that, under the climatic conditions that have prevailed, suppression attempts have been quite successful.

Prescribed burning and incendiarism were used by the recent Indian cultures of North America for agriculture, food gathering, hunting, and warfare, with the frequency and purpose showing wide geo-

graphic variations (Stewart 1956, Komarek 1967, Hough 1926). Archeological records show that prehistoric man has occupied the Yellowstone area as a hunter-gatherer for at least 10,000 years BP (Wedel et al. 1968, Lahren 1971). Small resident groups of American Indians, the Tukudika, and various Plains tribes traveled and hunted the greater Yellowstone area until the 1870's. Russell (Haines 1965) described an 1835 attempt by Blackfoot Indians in the Yellowstone area to drive his party of furtrappers from concealment by setting fire to the vegetation. Doane (Bonney and Bonney 1970) considered that the large 1870 fire had been set to drive game, and Gillette (1870) specifically attributes this fire to Indians. It seems probable that aboriginal man contributed to the frequency of fires on the area, but a quantitative assessment of this contribution is not possible.

The earliest recorded exploration of the Yellowstone area by Euro-American man in 1807-08 was followed by a period of fur trapping from about 1826-40. Osborne Russell's (Haines 1965) detailed journal suggests that trappers probably had little influence on fire frequency. Except for transient miners in the 1860's, the Yellowstone area remained poorly known until organized scientific exploration began in the late 1860's and early 1870's, with the park established in 1872. Fire suppression attempts began with the administration of Yellowstone Park by military personnel in 1886 (Harris 1886). Regular fire patrols were instituted and suppression activities increased until by the summer of 1889 Boutelle (1890) reported that "Seventy fires are known to have occurred in the park, all of which, except three, were extinguished." The removals of resident Indians and disruption of surrounding Plains cultures by 1880 should be considered an additional influence on fire frequency by Euro-American man.

Taylor (1969) has traced the development of more recent fire suppression activities in the park. Effectiveness appears to have increased with greater expenditures of manpower and with improvements in technology. The latter has included deployment of fire lookouts with a sophisticated communications network and has culminated in the use of aircraft (by 1939) and chemical retardants (by 1960).

Modern man has also had a potential for adding to the fire frequency on the area. Taylor (1973) found that 43% of 1,298 fires occurring in the park 1930-1970 were man-caused. Ninety-six man-caused fires occurred on the study area from 1931 to 1971. These were suppressed; only four burned 4 or more ha, with by far the largest recorded at 185 ha. These records suggest that, under the climatic conditions which have prevailed, man has been able to almost completely suppress fires on the grasslands of the

accessible study area for at least 30 years, and has substantially reduced the frequency of natural fires for as long as 80 years. (This interpretation may not apply to the more inaccessible forest areas in the remainder of the park.)

DISCUSSION

Data from this study have provided strong support for the hypothesis that wildfires have been a substantial influence on plant succession in this area of Yellowstone Park. Fire scars are a relatively crude measure of frequency and may underestimate the past influence of fire in this ecosystem because they may be formed only under favorable circumstances, such as by particularly severe fires. The best interpretation may be that much of the area would have burned at least one to four times since establishment of the park were it not for the actions of modern man. Changes that have occurred in the vegetation seem best explained by a reduction in fire frequency but have also occurred within a fluctuating climatic regime (Bray 1971) and with concomitant foraging by herbivores. Separation of these various influences is not entirely possible, and the following interpretations are regarded as tentative. In general, the reduced fire frequency has resulted in greater expressions of "climatic climax" vegetation (Daubenmire 1968b) than would otherwise be present. This is undesirable in a natural area, but if fire were reintroduced it appears to be possible to return some plant communities to more natural conditions.

The conspicuous increase of fire-sensitive *Artemisia tridentata* in the steppe (Fig. 1) would certainly be reversed if fire were reintroduced, and some changes in the relative abundance of herbaceous species might also be expected (Daubenmire 1968a, Conrad and Poulton 1966). Forest succession on the area has changed the relative abundance of species and increased the density and distribution of forests. Conifers have increased and aspen—the only significant deciduous species—has declined. Conifer succession could certainly be returned to more natural stages if fire were reintroduced. Aspen clones were estimated to occur on 2%-4% of the area, and 21 of the 31 scarred fir trees used in this study were also felled within 45 m of aspen, suggesting that aspen had formerly been subjected to frequent burning. Aspen in the Rocky Mountains reproduce mainly by vegetative means and may require periodic burning to stimulate reproduction (Loope 1972). Clones that have been entirely replaced by conifers or that are now represented by only scattered overmature trees have almost certainly been lost. It seems improbable that other remnant stands with understories now dominated by the exotic grass *Phleum pratense* would respond to burning. This grass has completely

altered composition of the understory vegetation and perhaps affected the pattern of ungulate foraging. Certain of these stands which occurred on forest-steppe ecotones and along floodplains may well have represented seral communities whose replacement was a natural event, but the reduction in fire frequency no doubt hastened the process. Finally, there are clones that might be expected to regenerate following fire, although this could be complicated on some sites by the foraging of herbivores. The relations between aspen and herbivores in this area are complex and controversial. Past workers have attributed the decline of aspen to the foraging of beaver (*Castor canadensis*) (Warren 1926) or elk (*Cervus canadensis*) (Kittams 1948, Barmore 1967).

A variety of information suggests the hypothesis that reduction in aspen has been primarily a function of reduced fire frequency, rather than of foraging by ungulates, particularly elk. The present clones, composed of large overmature trees ranging in age from about 75 to 120 years would formerly have been uncommon, as they would have been maintained in younger age distributions by frequent firing. Aspen appears to represent a food source for ungulates that is quantitatively so small in comparison with other forage sources that there is virtually no measurable feedback between ungulate population levels and aspen utilization. (A 60%–70% reduction in the elk population failed to significantly reduce utilization or achieve regeneration of aspen.) Palatable vegetation types with this relation to ungulate populations may persist only if they grow on favorable sites in vigorous condition. Fire probably maintained aspen in such condition. Gruell and Loope (*personal communication*) found that burned aspen clones reproduced successfully on ungulate winter ranges in Jackson Hole, Wyoming, immediately south of Yellowstone Park, but that successful reproduction generally continued for only 10–20 years following fires in areas of heavy browsing, and that unburned stands began to deteriorate after about 80 years. A 2.3-acre prescribed burn conducted during September 1966 on a 5-acre aspen clone on the present study area resulted in some initial increases in sprouting, but the light burn failed to kill the majority of the overstory trees, and sprouts did not grow vigorously (Barmore 1968). Because of the small amount of aspen relative to herbivore populations and the possible changes in hydrology discussed below, it seems probable that hot fires which kill most overstory aspen trees over relatively large areas will be necessary to adequately test hypotheses on the effects of ungulate browsing.

The reduced fire frequency has probably contributed to subtle changes in other vegetation types. The addition of a big sagebrush canopy on formerly

open grasslands and an increase in density and distribution of forest types could have changed the hydrologic characteristics of the smaller streams on the area (Sopper and Lull 1967, Tabler 1968, Hutchinson 1965). This in turn may have affected distribution of riparian vegetation such as willow (*Salix* spp.), alder (*Alnus tenuifolia*) and, on certain sites, aspen.

A detailed assessment of the reduction in fire frequency on the relations between herbivores and their habitat in Yellowstone Park will be the subject of future papers, but in view of the controversy surrounding the park's ungulate fauna some additional comments are pertinent. Wildfires have been a major abiotic influence on the winter forage supplies of these ungulates, and in combination with similar influences, such as drought and severe winters, have probably had short-term effects on ungulate distribution and population dynamics. Interpretations of "overgrazing" or of departures from natural conditions of vegetation due to foraging by native ungulates cannot be valid in a natural area until the influences of wildfire have been evaluated.

Quite obviously the effects of fire on plant succession and upon ungulate habitat relations could be tested by again allowing natural fires to burn. An initial step in this direction was taken in 1972 by establishing over 122,000 ha of Yellowstone Park, including about 12,000 ha of the study area, as two zones where natural fires were allowed to run their course. Four very small fires burned in these zones during the summer of 1972, but none occurred on the study area.

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FIRE AND LANDSCAPE DIVERSITY IN SUBALPINE FORESTS OF YELLOWSTONE NATIONAL PARK¹

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Abstract. Fire history was determined by fire scar analysis in a 73-km² subalpine watershed in Yellowstone National Park, Wyoming, USA. Evidence was found for 15 fires since 1600, of which 7 were major fires that burned >4 ha, destroyed the existing forest, and initiated secondary succession. Most of the upland forest area was burned by large, destructive fires in the middle and late 1700's. Fires since then have been small and have occurred at long intervals. Fire frequency in this area is partly controlled by changes in the fuel complex during succession. Fuels capable of supporting a crown fire usually do not develop until a stand is 300–400 yr old, and ignitions prior to that time usually extinguish naturally before covering more than a few hectares. Thereafter a destructive crown fire is likely whenever lightning ignites small fuels during warm, dry, windy weather. On the extensive subalpine plateaus of Yellowstone National Park there appears to be a natural fire cycle of 300–400 yr in which large areas burn during a short period, followed by a long, relatively fire-free period during which a highly flammable fuel complex again develops. The 73-km² study area appears to be about midway between major fire events in this cycle. This, rather than human fire suppression, apparently is the major reason for the small number and size of fires in the area during the last 180 yr.

On the basis of the fire history data, the sequence of vegetation mosaics during the last 200 yr was reconstructed for the watershed. Indices of landscape diversity were computed for each reconstruction, treating forest types and successional stages as taxa and incorporating components of richness, evenness, and patchiness. Landscape diversity was highest in the early 1800's following the large fires in the 1700's, then declined in the late 1800's and early 1900's during a 70-yr period when no major fires occurred and the landscape was dominated by even-aged forests developing on the areas burned in the 1700's. Landscape diversity has increased somewhat during the last half-century as a result of two small fires and the effects of the mountain pine beetle. These landscape reconstructions for the last 200 yr suggest that the Yellowstone subalpine ecosystem is a nonsteady-state system characterized by long-term, cyclic changes in landscape composition and diversity. Such cyclic patterns may significantly influence wildlife habitat, streamflow, nutrient cycling, and other ecological processes and characteristics within the Park, and they may be an important consideration in judging whether recent ecological changes are natural or man induced.

The landscape reconstructions were also made using a simulation model based on hypothetical fire management policies of total fire exclusion and selective fire control (permitting only small fires to burn). These hypothetical management policies generally reduced the richness and patchiness of the landscape compared to the natural fire regime, but they increased the evenness and reduced the magnitude of periodic fluctuations in overall landscape diversity. At times, overall landscape diversity may actually be higher with a fire control policy than with a natural fire regime. At other times, fire significantly increases landscape diversity, as would be expected.

Key words: fire; fuels; landscape diversity; lodgepole pine; mathematical model; mountain pine beetle; steady state; subalpine forest; succession; Yellowstone National Park.

INTRODUCTION

The measurement and interpretation of diversity have long interested biologists. Most work has focused on the diversity of species in communities, but, as Pielou (1975) points out, diversity exists and can be treated at many levels of biological organization. In this paper I present an analysis of vegetation diversity at the landscape level, i.e., the diversity of plant communities comprising the landscape of a 73-km² watershed in Yellowstone National Park, Wyoming,

USA. Because of the importance of fire as a natural ecosystem perturbation in this area, the emphasis is on diversity patterns resulting from a variety of possible fire management policies ranging from a natural fire regime to complete fire exclusion. In this context, landscape diversity must be viewed as resulting from the superposition of two different vegetation patterns: (1) patterns related to the distribution of species along gradients of limiting factors, and (2) patterns resulting from portions of a landscape being in different stages of recovery following disturbance (Reiners and Lang 1979). The relative contribution of these two kinds of patterns to overall landscape diversity varies. In desert mountain ranges, for instance, pronounced resource gradients control community composition and distribution (Whittaker and Niering 1965). Other land-

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scapes have a comparatively uniform abiotic environment, but periodic fire maintains a mosaic of successional stages (Lawton 1978).

Two components of diversity are generally recognized: richness, or the number of distinct taxa present, and evenness, or the distribution of individuals among those taxa (Peet 1974, Pielou 1975). These concepts of species diversity can also be applied to the diversity of communities in a landscape. Thus, the richness of a landscape can be defined simply as the number of different community types present, including those types differentiated by their position on environmental gradients as well as successional stages in a particular sere. The evenness of a landscape can be expressed as the proportion of the total area covered by each community type, maximum evenness occurring when every type occupies an equal area. Another important consideration in landscape diversity is the size and interspersal of individual community units. A landscape with three community types distributed in many small patches appears more diverse than a landscape with the same three community types in a few large blocks. Therefore, I also treated a third diversity component related to the interspersal and contrast of communities, a patchiness component.

In areas where fire was an important natural disturbance prior to European settlement and where management now emphasizes preservation of primeval conditions, there is concern that recent fire control policies may have reduced landscape diversity and created an unnatural situation. The amount of land covered by early postfire successional stages appears to have declined in some areas, with older stages increasingly dominating the landscape (Habeck and Mutch 1973, J. R. Habeck, *personal communication*). This concern is a major impetus for the current development of new fire management plans, which propose to return fire to the system either by permitting some lightning-caused fires to burn or by using controlled prescribed burning (Kilgore 1976, Mutch 1976). It is important now to assess the degree to which different ecosystems have been altered by past fire control policies, to determine the urgency with which fire should be reintroduced, and to judge the effectiveness of specific fire management plans. In areas where fire formerly occurred frequently, its exclusion may soon produce obvious changes in vegetation structure and species composition (Cooper 1960, Loope and Gruell 1973, Lunan and Habeck 1973, Humphrey 1974, Kilgore and Taylor 1979). However, in other areas where fire occurred naturally at longer intervals, significant impacts may be more difficult to detect because of the problem of distinguishing between landscape changes attributable to fire control and those resulting from other normal dynamic processes. In fact, 50–100 yr of fire suppression may have had little effect in some ecosystems characterized by infrequent fire (Clagg 1975, Pickford et al. 1980). Therefore, a major objec-

tive of this study was to determine the degree to which natural landscape patterns in subalpine portions of Yellowstone National Park have been altered by modern fire control.

My approach to this problem was to reconstruct long-term patterns in landscape diversity prior to the influence of European man (pre-1880), then to determine how long it would take for significant departures from these natural patterns to occur under a variety of possible fire management policies. Thus, there were three parts to the study. First, I used fire scar analysis to determine the frequency and size of fires during the last 350 yr in a representative watershed of 73 km², undisturbed except for recent fire control. I then sampled dead woody fuels in a chronosequence of stands ranging from early to late successional stages, both to test Despain and Sellers' (1977) hypothesis that the average interval between successive fires on a single site is partly controlled by development of a fuel complex capable of supporting a crown fire, and to obtain a better estimate of this mean fire interval. Finally, using these fire history data, I reconstructed the vegetation mosaics that must have existed in this watershed during the last 200 yr, and developed a computer model to simulate temporal landscape changes under various regimes of fire size, frequency, and management policy.

STUDY AREA

The study was conducted in the 73-km² Little Firehole River watershed, located west of Old Faithful on the Madison Plateau, a relatively flat Quaternary lava flow covering several hundred square kilometres in west-central Yellowstone National Park, Wyoming (Fig. 1). Plateau rhyolite forms the bedrock throughout, covered by sandy glacial till and kame deposits on the uplands and fine-grained alluvium along streams and moist meadows (United States Geological Survey 1972a, b). Except for a deep, narrow canyon cut by the Little Firehole River, the eastern and northern portions of the watershed are relatively flat, with an average elevation of 2450–2500 m. Numerous small hills and depressions create some local relief, generally of 25 m or less. To the west and south the land slopes upward to 2650 m, with generally moderate inclines but a few steep slopes and talus fields. In contrast to other parts of the Rocky Mountains where rugged topography may exert a major influence on fire behavior, the relatively uniform topography and geologic substrate of this watershed afford a good opportunity to study long-term fire cycles in relation to vegetation structure and fuels.

No weather stations exist within the study area, but an isohyet map constructed for Yellowstone National Park (Dirks and Martner 1978) indicates a sharp precipitation gradient from ≈100 cm annually in the eastern and northern portions of the watershed to ≈150 cm in the southern and western parts. Most of the

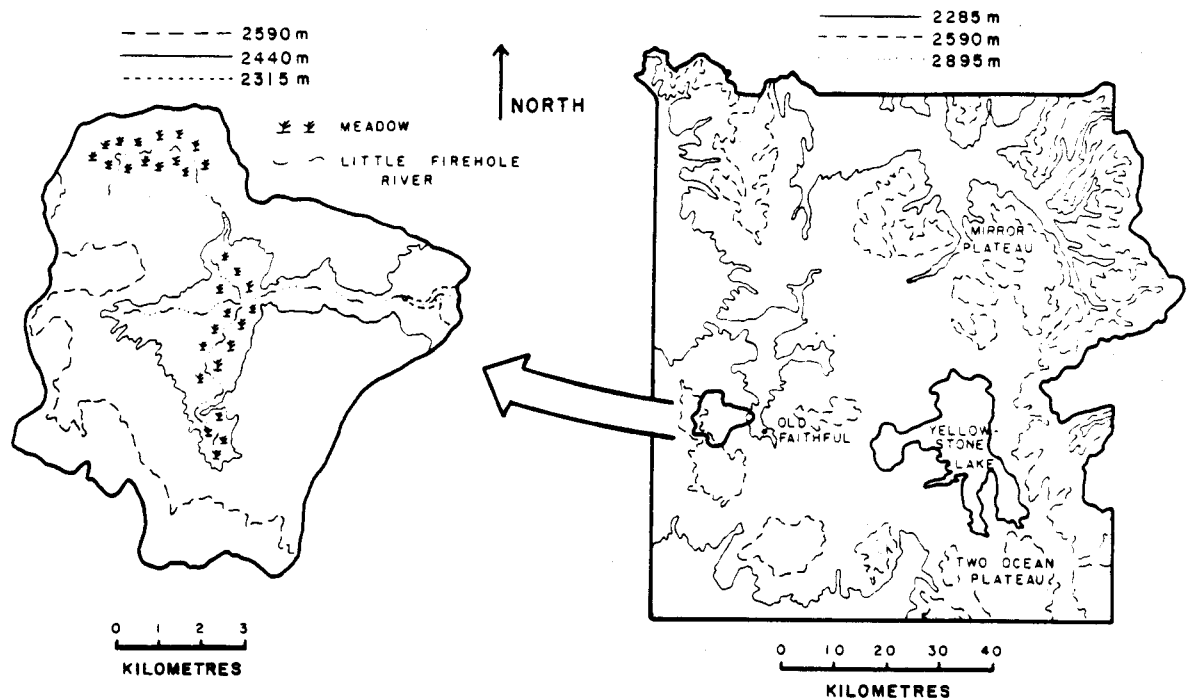


FIG. 1. Map of Yellowstone National Park, showing the location of the study area, and a map of the Little Firehole River watershed, showing major topographic features.

watershed receives ≈ 125 cm annually, slightly more precipitation than occurs in most of the Yellowstone subalpine zone. Winters are long and cold, with maximum daytime temperatures often below freezing (Dirks and Martner 1978). Summers are short and mild, with maximum daytime temperatures around 21°C and occasional nighttime frosts. Prevailing winds are from the southwest.

I developed a classification of plant community types based on the habitat types and forest successional stages present in the watershed (Table 1). A habitat type (HT) is an aggregation of land units capable of producing similar climax vegetation and usually named after the dominant climax tree and a dominant or characteristic herb or shrub. I recognized two major upland habitat types, modified slightly from a preliminary classification of forest habitat types in eastern Idaho and western Wyoming prepared by the United States Forest Service Intermountain Region (R. Steele, D. Ondov, S. V. Cooper, and R. D. Pfister, personal communication). The *Pinus contorta*/*Carex geyeri* (Pico/Cage) habitat type occupies ≈ 25 km² in the drier eastern and northern portions of the watershed. Lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) dominates both pioneer and climax forest stages. The *Abies lasiocarpa*/*Vaccinium scoparium* (Abla/Vasc) habitat type occupies ≈ 36 km² in the more mesic western and southern parts of the watershed. Here lodgepole pine again dominates early successional stages, but shares dominance with subalpine fir

(*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry), and whitebark pine (*Pinus albicaulis* Engelm.) in the climax.

Postfire succession is similar in the two upland habitat types. The successional continuum can be divided into six relatively distinct stages (modified from Despain 1977) that are supported by cluster analysis of structural characteristics in 18 upland stands (Romme 1979: Appendix 4). There is little difference in appearance or structure between the Pico/Cage and Abla/Vasc habitat types in the first five successional stages. Though herbaceous species composition may differ somewhat, functional parameters of productivity, transpiration, nutrient cycling, wildlife habitat, and fire susceptibility probably are similar. Therefore, I treated both habitat types together in the first five successional stages (Table 1:1–5). The two climax forests are significantly different in structure and function, however, and are classified as distinct communities.

The initial herbaceous stage (Table 1) is dominated by common forest floor species that resprout vigorously from undamaged underground parts (Lyon and Stickney 1976) plus a few species that are absent or rare in mature forests (Taylor 1969). Large fire-killed stems are numerous, both standing and fallen, but small woody material is sparse.

During the second successional stage the stand becomes dominated by seedlings and saplings of lodgepole pine, although herbs remain abundant. Most of

TABLE 1. Community types in the little Firehole River watershed, with age intervals for types 1-7, which represent the postfire successional stages in the two major upland habitat types. Subalpine meadow (8), riparian forest (9), and steep-slope forests (10) are additional recognized habitat types, but these remained relatively stable in composition and structure. The column headings under each habitat type refer to variations in the general pattern of forest succession after fire. See Study Area in text for description of habitat types and explanations of the various successional patterns and age intervals.

Community type	Age in years						
	Pico/Cage habitat type*				Abla/Vasc habitat type†		
	Typical stands	Slow restocking	Early pine canopy mortality	Late pine canopy mortality	Typical stands	Early pine canopy mortality	Late pine canopy mortality
1. Herbaceous stage	0-20	0-40	0-20	0-20	0-20	0-20	0-20
2. Seedling-sapling stage	20-40	40-80	20-40	20-40	20-40	20-40	20-40
3. Immature-pine forest stage	40-150	80-200	40-150	40-150	40-150	40-150	40-150
4. Mature-pine forest stage	150-200	200-250	150-170	150-300	150-300	150-180	150-350
5. Transitional stage	200-300	250-350	170-240	300-400	300-400	180-280	350-450
6, 7. Climax forest: Pico/Cage HT. Abla/Vasc HT	300+	350+	240+	400+	400+	280+	450+

* *Pinus contorta*/*Carex geyeri* habitat type (more xeric upland sites).

† *Abies lasiocarpa*/*Vaccinium scoparium* habitat type (more mesic upland sites).

the pine seedlings usually become established during the first several years to form an even-aged cohort that will dominate the stand for several decades. Large standing and fallen fire-killed stems remain prominent throughout this stage, though small dead woody material is still sparse.

The third successional stage includes the time from initial canopy closure through maturation of the even-aged pine cohort. It is characterized by rapid tree growth and extensive self-pruning of lower limbs plus thinning in dense stands. Herbaceous production and diversity decline sharply during this stage (Taylor 1969). Most of the large fire-killed stems fall and decompose during this time, and duff and litter begin to accumulate on the forest floor in greater quantities. The resulting mature pine forest, which forms the fourth successional stage, has a single, dominant, even-aged canopy stratum and a very open understory. The stand appears to change relatively little during this fourth stage, although a sparse understory of fir and spruce begins to develop on sites capable of supporting these more shade-tolerant species. Annual wood increments in the dominant pine are very small.

Extensive mortality eventually appears in the even-aged pine canopy, marking the onset of the fifth successional stage. In the Abla/Vasc habitat type the former lodgepole dominants are gradually replaced by fir, spruce, and whitebark pine from the developing understory. A second generation of lodgepole pine also becomes established in gaps; thus this species persists in the stand but is no longer the exclusive canopy dominant. In the drier Pico/Cage habitat type the disintegrating canopy is replaced by second-generation lodgepole pine and some whitebark pine. This transitional stage is marked by a well-developed understory and a relatively sparse canopy, with numerous large, dead stems, standing and fallen.

The sixth successional stage is the climax forest,

containing trees of many different size- and age-classes. The initial, even-aged lodgepole pine cohort has completely disappeared from the canopy, and stand structure and composition appear to remain relatively constant until the next major disturbance.

The rate of succession in the two upland habitat types varies in response to local site conditions and disturbance history. The seral stage endpoints in Table 1 are based on my observations of the relationship between stand age and successional stage in >100 stands located throughout the study area. Obviously changes in stand structure and composition are gradual and continuous rather than abrupt, as implied by this table, but a discrete classification was necessary for the analysis of landscape diversity. The greatest variation in the rate of succession is due to differences in the initial reestablishment of trees after a fire and in the onset of extensive mortality in the mature, even-aged lodgepole pine canopy. Tree age data from this study show that the even-aged lodgepole pine cohort usually became established within the first several years after a fire (Table 1: Typical stands). However, initial tree establishment sometimes occurred over 30 yr or more, producing only broadly even-aged stands, particularly in the drier Pico/Cage habitat type. Such slow restocking may be due to summer drought (Patten 1963, J. R. Habeck, *personal communication*), herbaceous competition (Stahelin 1943, Langenheim 1962), or inadequate seed source, for most cones in this area are nonserotinous.

The onset of extensive mortality in the mature, even-aged pine canopy is generally earlier in the Pico/Cage habitat type than in the Abla/Vasc habitat type, due to the effects of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and a second unidentified mortality agent. The pine beetle selectively kills the larger trees in a stand by feeding and constructing egg galleries in the phloem. Trees on drier sites at

lower elevations are most vulnerable (Amman et al. 1977). Beetles sometimes cause early canopy mortality in the more mesic Abia/Vasc habitat type, but their effect is most widespread in the Pico/Cage habitat type where the mature pine forest stage (Table 1) usually lasts only a few decades compared to a century or more on other sites. Observations of recently killed trees indicate that a low to moderate beetle population presently exists in the Pico/Cage habitat type in the Little Firehole River watershed. A destructive beetle epidemic has occurred during the last decade in southwestern Yellowstone National Park and in a large adjacent area to the south and west. Photographs of the Old Faithful area in the late 1800's show numerous dead trees in the forest, possibly killed by pine beetles.

The second type of early canopy mortality, whose cause is unknown at this time, occurs most often in dense stands on dry sites within the Pico/Cage habitat type. It produces widespread patches, usually ≤ 1 ha in area, in which almost all canopy trees have died, including smaller trees as well as larger ones. The bark on the lower 1–2 m of stem in affected trees appears to first separate from the wood, later to crack and peel away. The tree dies eventually after the bark has been lost around the entire circumference. Some trees have similar lesions near the top of the stem. The causative agent appears to be a stem or root fungus, although no organism has been isolated. Many pathogenic fungi are known to be associated with lodgepole pine in this region (Nordin 1954, Shaw 1973).

In addition to the two upland habitat types described above, I recognized three other habitat types in the watershed that appear to change relatively little with time. These comparatively stable habitat types together comprise $\approx 16\%$ of the total watershed area. Subalpine meadows cover ≈ 7 km², mainly on alluvial soils. Other alluvial and riparian sites support open forests of lodgepole pine, subalpine fir, and Engelmann spruce with a rich herbaceous ground cover. Although some fire-scarred trees can be found in these riparian forests, fires apparently have been less frequent and less destructive here than in the upland habitat types. Riparian forests, which cover ≈ 4 km², appear relatively stable in composition and structure, with no obvious secondary successional trends. Finally, small rock outcrops, boulder fields, and steep, rocky slopes cover ≈ 1 km² and support sparse forests of pine, fir, and spruce.

Human disturbance in the Little Firehole River watershed is minimal. Two foot trails in the area receive moderately heavy use, but away from the trails evidence of man is rare. A preliminary archaeological investigation of Yellowstone National Park by D. C. Taylor in 1964 (*personal communication*) shows that prehistoric man was present in the geyser basins a few kilometres to the east, but there is no reported evidence of human activity in the study area. Although

attempts have been made to control fires since 1886 (D. B. Houston, *personal communication*), fire suppression on the forested subalpine plateaus probably was not very effective until well into the 20th century when mobilization and suppression techniques greatly improved. Records show only one fire in the study area during Park history, an 88-ha burn that was suppressed in 1949 (Taylor 1969). Since 1975 a new fire management plan has been in effect which permits lightning-caused fires to burn without interference in wilderness portions of the Park (including the Little Firehole River watershed) if human life, property, or other values are not threatened.

METHODS

Fire history

The frequency and areal extent of past fires was determined by use of fire scar methods developed by Heinselman (1973) and Arno and Sneek (1977). Living fire-scarred trees were located and sectioned with a bow saw. An attempt was made to date fire scars with an increment corer, but only very approximate dates (± 20 yr) could be obtained. Lodgepole and whitebark pine with single fire scars were found frequently, but multiscarred trees were uncommon. Care was taken to distinguish fire scars from scrape scars, bear-feeding scars, and other forms of injury (Molnor and McMinin 1960).

In the laboratory the fire scar sections were sanded, wetted, and the rings counted under a $10\times$ microscope. False or partial rings were not evident, but the rings in old trees frequently were extremely small and difficult to count even with careful sanding and wetting. In some sections it was also difficult to determine exactly which ring corresponded to the fire year. These problems, plus the fact that the rings were not cross-dated with a master tree ring chronology, resulted in some dating errors. In general, fire years reported here within the last 100 yr are ± 2 yr, between 100 and 200 yr ago: ± 3 yr, and over 200 yr ago: ± 5 yr. This method appears to give reliable estimates of past fire years within the limits of error in ring counts. Each of three fire-scarred trees sampled in 1978 from an area known to have burned in 1949 had 29 annual rings between the cambium and the ring just beneath the scar. Two fire-scarred trees from an area known to have burned in 1901 (located 2.5 km east of the Little Firehole River study area) also gave fire dates of 1900 and ≈ 1900 , the rings being difficult to count in the latter.

In addition to the sampling of fire-scarred trees, increment cores were taken from several dominant lodgepole pine (*Pinus contorta*) to document postfire reproduction. Lodgepole pine is the major shade-intolerant species restocking recently burned sites in this area. Cores were taken as close to the base as possible (usually at ≈ 20 cm), and an estimate of age at coring height was added to the number of rings on the core.

TABLE 2. Categories of dead woody fuels (after Brown 1974, Deeming et al. 1977, Despain and Sellers 1977). Time lag (TL) refers to how rapidly fuel moisture responds to changes in atmospheric humidity, i.e., the time necessary for a fuel particle to lose 63% of the difference between its initial moisture content and its equilibrium moisture content.

Fuel category	Units	Description	Major effect on fire behavior
A. Needle litter depth	mm	Undecomposed needles, twigs, cone scales, and other small particles on the ground	Fuels supporting ignition and initial surface spread
1-h time lag fuels (1h TL)	kg/ha	Dead, woody pieces ≤ 0.635 cm diameter	
B. Total fuels	kg/ha	Dead, woody pieces of all sizes	Fuels contributing to intensity (heat release) and flame height
C. 1000-h time lag rotten fuels (1000-h TL rotten)	kg/ha	Dead, woody pieces > 7.5 cm diameter in early stages of decomposition (form still easily recognizable)	Fuels in which fire may persist during periods of damp weather, in which fire brands may ignite spot fires, and which contribute to heat release in intense fires
Duff depth	mm	Decomposing organic matter, origin unrecognizable, lying above mineral soil and below litter	

This estimate of age at coring height, based on the width of the innermost rings, ranged from 3 yr/20-cm height in trees with very wide rings (4–6 mm) to 20 yr/20-cm height in trees with very narrow rings (≤ 1 mm). These values were obtained by sampling several fast- and slow-growing saplings both at the base and at a height of 20 cm. Dominant Engelmann spruce (*Picea engelmannii*), whitebark pine, (*Pinus albicaulis*), or subalpine fir (*Abies lasiocarpa*) were aged in some late-successional stands. Fire scar sections and/or increment cores were obtained in 92 stands distributed throughout the watershed. Fire-scarred trees could not be found in 56 of the stands.

The areal extent of past fires was determined by mapping even-aged lodgepole pine forests of fire origin. Where burns had created distinct forest discontinuities, the precise boundaries were transferred from color aerial photographs taken in 1969 and 1971 to a base map, using a zoom transfer scope. Stands differing in age by > 100 yr usually could be distinguished on the photographs. With smaller age differences, however, variations in forest structure often were related more to topographic and other effects than to stand age. In these situations the boundaries were located in the field.

Fuel accumulation

To evaluate the likelihood of fire in relation to stand age, fuels were sampled in 16 upland forest stands representing a chronosequence from age 29 to 550+ yr. All stands were located on similar soils and substrata, with most on flat or gently sloping terrain. There was some variation in elevation (2365–2550 m) and site productivity (site index, a relative measure of potential site productivity that is defined as the average height (in feet) of dominant trees at age 100 yr, was 40–80, with most 50–60), but stand age was not

correlated with these factors (Romme 1979; Appendix 2). The planar intersect method (Brown 1974) was used to sample the several components of the total dead fuel complex, each of which has a major influence on a particular aspect of fire behavior (Table 2). Intersections along 20 transects were counted in each stand, resulting in coefficients of variation [(standard error/ $\bar{x}$) $\times 100$] of 10–20% for duff and needle litter, 10–35% for small particles (up to 7.5-cm diameter), and 15–60% for large material (> 7.5 -cm diameter). Site index was determined directly in lodgepole pine-dominated stands that were 30–200 yr old (Alexander 1966). In stands outside this age range, an estimate of site index was obtained by assigning the value of a nearby stand to a similar site or by extrapolating the site index tables.

Forest fuels are sometimes envisioned as increasing steadily with time, but several patterns are possible and each fuel component may change differently (Brown 1975). Therefore fuels data were first plotted against stand age. For time periods where an apparent change in a fuel component coincided with events in the development of a forest stand that could be expected to produce such a change, the relationship of fuels to stand age was tested statistically. For example, heavy fuels (> 7.5 cm) would be expected to decrease during early successional stages as large fire-killed stems decompose, then to increase in later stages when natural mortality of mature trees begins to occur. A plot of heavy fuels vs. stand age does show this pattern. A stepwise linear regression was calculated for each stand age interval, with fuels (kilograms per hectare) as the dependent variable and stand age and site index as the two independent variables. Where a significant nonzero slope was obtained with stand age as the first independent variable in the regression, it was concluded that fuels increase or de-

crease during the stand age interval tested. Where the slope was not significantly different from zero or where site index was the first independent variable, no change in fuels attributable to stand age was assumed.

Fuels data from two representative stands in the Pico/Cage and Abia/Vasc habitat types in the Little Firehole River watershed, 350 and 450 yr old, respectively, were used in Rothermel's (1972) computer-based fire behavior simulation model with the assistance of the United States Forest Service Northern Forest Fire Laboratory in Missoula, Montana, USA. This model predicts fire intensity and rate of spread based on the mass and moisture content of small dead woody fuels (≤ 7.5 -cm diameter), needle litter, and live fuels. The model is limited by its assumptions of a homogeneous fuel bed and noncrowning surface fire (Albini 1976), but when interpreted in conjunction with other data and observations its results provide an additional basis for predicting the kinds of fires likely to occur in this area.

Landscape reconstruction and simulation

A common approach for reconstructing past vegetation patterns is to use descriptions in original land survey records (Peterken 1976, Gross and Dick-Peddie 1979, Rodgers and Anderson 1979) or old photographs and journals of early explorers (Progulske 1974, Gruell 1980a, b, D. B. Houston, *personal communication*). Such historical documentation was not available for the Little Firehole River watershed, but my data on fire history and forest succession in the area permitted a reconstruction of vegetation mosaics existing as much as 200 yr ago (cf. Henry and Swan 1974). For example, to re-create the landscape of 1778 I made a map showing the age (time since the last destructive fire) of all forest stands in 1978 and subtracted 200 yr from each. On the resulting map of stand ages in 1778, I then determined the successional stage of each stand, based on observations of the relationship between stand age and successional stage in the watershed today. I assumed that rates and patterns of succession in the recent past were similar to those of today. Although there is evidence that the Yellowstone area was slightly cooler and possibly wetter 200 yr ago (D. B. Houston, *personal communication*), I believe the error attributable to climatic change is minor.

My approach to landscape reconstruction was straightforward except in two types of situations. The first involved stands that had burned more recently than the date of interest (e.g., areas that burned in 1795 on the reconstruction for 1778). My fuels data indicated that destructive fires in the subalpine forests of Yellowstone Park are most likely in late successional stands (see Results: fire history). Moreover, several recent, uncontrolled fires in the Park that burned intensely in old forests (350+ yr old) have been observed to become diminished in intensity and rate of spread or even to stop when they reached younger

stands (100 yr old), despite continued favorable weather conditions (Despain and Sellers 1977, D. G. Despain, *personal communication*). Therefore, for my reconstructions I assumed that each area was in the climax stage when it burned. However, it was impossible to know exactly how old a stand was when it burned, so interpretation of forest history on a site long before the last destructive fire was somewhat speculative. Because a major fire burned a large portion of the watershed in 1795, I felt confident about recreating detailed vegetation mosaics only as far back as 200 yr ago (1778), with more generalized reconstructions for the early and mid-1700's.

A second problem was estimating the present age of climax stands in which the even-aged lodgepole pine (*Pinus contorta*) that initially recolonized the site after the last destructive fire have long since disappeared along with any fire-scarred trees. Such areas comprise $\approx 20\%$ of the watershed, and although they are in the climax stage today they may have been in earlier successional stages 200 yr ago. It is probably impossible to determine the exact stand age in these situations, but by considering the changes in fire risk as forest stands mature, as well as site-specific differences in average fire frequency, it was possible to make a reasonable estimate of present stand age. Moist, sheltered sites, such as some drainage bottoms and northeast-facing slopes, probably burn very infrequently (Quirk and Sykes 1971, Habeck 1976, Romme and Knight 1981), and therefore I assumed that climax stands on these sites have been in this stage throughout the last 200 yr. However, it seems unlikely that climax stands developing on less-protected sites (ridgetops, etc.) would persist very long, for the fuel characteristics in climax stands confer a high fire risk in an area where summer lightning storms are common. These stands are generally surrounded by younger stands of known age, usually separated by a sharp discontinuity. As noted above, recent uncontrolled fires in Yellowstone Park that burned rapidly and intensely through old-growth forests have been observed to stop when they reached a younger forest stand, apparently because of changes in the fuel complex rather than wind, moisture, or other external factors (Despain and Sellers 1977). If it can be assumed that similar fire behavior in the past was responsible for the distinct forest discontinuities observable today, then most stands that are presently in a climax stage must have been in an earlier stage at that time in the past when an intense fire burned to their borders and stopped. Because high fire risk develops around age 350 yr in forests of this area (see Discussion), today's climax stands must have been no more than 350 yr old at the time of the most recent adjacent burn. Therefore I added 350 yr to the age of the most recent adjacent burn to arrive at a maximum likely stand age today. Of course the stand may have been much less than 350 yr old at the time of the adjacent fire: a minimum likely

TABLE 3. Landscape diversity indices.

1. Relative richness (<i>R</i>)	
$R = \frac{T}{10} \times 100$	where <i>T</i> = number of different community types present. (Maximum possible number is 10.)
2. Relative evenness (<i>E</i>)	
$E = \frac{H^2(j)}{H^2(\max)} \times 100$	where <i>H</i> ² (<i>j</i>) = modified Simpson's index (Pielou 1975) computed for landscape <i>j</i>
where	<i>H</i> ² (max) = maximum possible value of <i>H</i> ² for <i>T</i> community types
$H^2 = -\ln \sum_{i=1}^T p_i^2$	<i>P</i> _{<i>i</i>} = proportion of total landscape area covered by <i>i</i> th community type
	<i>T</i> = number of different community types present
3. Relative patchiness (<i>P</i>)	
$P = \frac{\sum_{i=1}^N D_i}{N} \times 100$	where <i>N</i> = number of boundaries between adjacent 5-ha cells in the watershed
	<i>D</i> _{<i>i</i>} = dissimilarity value for the <i>i</i> th boundary between adjacent 5-ha cells (Table 4)

stand age today would be the average age at which stands on the type of site in question first develop the characteristics of the climax stage (Table 1). For each climax stand on sites that are not sheltered topographically, I assigned the mean of this maximum and minimum estimate as the stand age in 1978 and used it for reconstruction of past landscapes.

This approach allows re-creation of the vegetation mosaic that existed at a particular time in the past. For a more continuous landscape reconstruction that also permits prediction of future vegetation mosaics, I developed a computer model that simulates succession and periodically calculates landscape diversity indices. I divided the 73-km² watershed into 1429 5-ha cells, constructed a basic model of forest succession, and applied it to each cell individually. Every cell was first assigned a habitat type, an initial stand age, and a set of ages representing seral stage endpoints (Table 1); these data were determined from the location of the cell in the watershed. An algorithm then determined the state of each cell, i.e., to which of 10 community types it belonged (Table 1). Cells in the two

upland forest habitat types (Pico/Cage and Abia/Vase) were classified according to stand age as one of seven community types representing successional stages. The other three community types represent habitat types in which community structure and composition remain relatively constant over time (riparian forest, meadows, and rocky slopes). The program summarized the state of all individual cells to determine the overall state of the watershed system and to calculate landscape diversity indices. An increment then was added to the age of each cell, and the process was repeated. I introduced fire into the system by returning certain 5-ha cells to age zero at specified times. As with the first approach to landscape reconstruction, this model assumes that rates and patterns of succession in the past and future are similar to those observable today (see Romme 1979: Appendix 3 for programming details).

Quantitative landscape diversity indices

To provide more meaningful diversity indices I expressed richness, evenness, and patchiness as relative indices, i.e., as a percent of the maximum possible value (Table 3). Thus, for the richness component I tallied the number of community types present and divided by 10, which is the total number of taxa recognized in the study (Table 1). To measure evenness I used Pielou's (1975) modification of Simpson's (1949) dominance index (Table 3). The maximum possible value of this index varies depending on the number of community types present and was computed separately for each case. For patchiness I modified Patton's (1975) habitat edge index which expresses the total perimeter of edge (boundaries between unlike plant communities) within a landscape area. To incorporate a measure of the contrast between adjacent communities in my patchiness index, I developed a table of dissimilarity values ranging from 0.0–1.0 based on my subjective evaluation of differences in physical structure and species composition (Table 4). Using this table, I determined the appropriate dissimilarity value for every boundary between adjacent 5-ha units in the computer model. Where two adjacent 5-ha units contained identical community types, the dissimilarity value for their boundary was 0. I then computed the patchiness index for the watershed by summing all of the individual dissimilarity values so determined, and dividing by the maximum possible dissimilarity value that would result if every pair of adjacent cells were maximally different (i.e., if every boundary received a value of 1.0; Table 3). A total of 2770 boundaries among 1429 5-ha cells was analyzed. Finally, I attempted to measure overall landscape diversity in two different ways. First I standardized the relative richness, evenness, and patchiness indices, giving equal weight to each, and averaged the three. Secondly, I computed the Shannon-Wiener diversity index (*H'*;

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TABLE 4. Relative dissimilarity values (0-1.0) for boundaries between adjacent community types. These are the possible values of D_1 used in computation of the patchiness index (Table 3).

	Herbaceous stage	Seedling-sapling stage	Immature-pine forest	Mature-pine forest	Transitional stage	Climax Pico/Cage forest	Climax Abia/Vasc forest	Riparian forest	Steep-slope forest	Meadow
Herbaceous stage	0	.5	.6	.7	.8	.9	.9	.9	.8	.8
Seedling-sapling stage		0	.4	.6	.7	.8	.8	.8	.7	.9
Immature-pine forest			0	.3	.4	.5	.5	.5	.4	1.0
Mature-pine forest				0	.4	.5	.5	.5	.3	1.0
Transitional stage					0	.3	.3	.3	.2	1.0
Climax Pico/Cage forest						0	.3	.3	.2	1.0
Climax Abia/Vasc forest							0	.3	.8	1.0
Riparian forest								0	0	1.0
Steep-slope forest									0	1.0
Meadow										0

Pielou 1975), using the percent of the watershed area covered by a community type as the measure of its abundance.

RESULTS

Fire history

Table 5 presents a master fire chronology for the Little Firehole River watershed, based on fire year determinations from 44 fire-scarred trees in 36 stands. Several fire years are represented by a cluster of sample dates, the variation apparently attributable to errors in ring counts. The fire year in these cases was estimated on the basis of the frequency distribution of sample dates plus the age of postfire lodgepole pine reproduction in affected stands. A total of 14 fires during the last 350 yr was documented by fire scars, and an additional fire around 1630 was suggested by the presence of extensive 350-yr-old stands of lodgepole pine (*Pinus contorta*). Of these 15 fires during the last 350 yr, 7 were major fires that covered 4 ha or more, destroyed the existing forest, and initiated secondary succession. The remaining 8 fires apparently covered very small areas and produced little change in the vegetation.

The frequency of major fires and of all fires during the last 350 yr, expressed as the number of fires per 100 km² per year (Romme 1980), was calculated separately for the Pico/Cage habitat type, the Abia/Vasc habitat type, and for the entire watershed including upland forests, riparian forests, and meadows (Table 6). To illustrate, for all fires in the Pico/Cage habitat type (data from Table 6),

$$\begin{aligned}\text{Frequency} &= (10-1) \text{ fires} \cdot 25.4 \text{ km}^{-2} \cdot 302 \text{ yr}^{-1} \\ &= 0.117 \text{ fire} \cdot 100 \text{ km}^{-2} \cdot \text{yr}^{-1}.\end{aligned}$$

The time period is the interval between the oldest and most recent documented fires; the number of fires in the calculation is one less than the total number occurring during that time. The units are fires per 100 km² per year rather than fires per square kilometre per

year to reduce the number of zeros in the results and to reflect the size of the area from which the data were obtained. For comparison, similar calculations were made using data from the Two Ocean and Mirror Plateaus in eastern Yellowstone National Park, where all lightning-caused fires since 1972 have been allowed to burn without interference (Sellers and Despain 1976, D. G. Despain, *personal communication*). Vegetation and climate here are similar to the Little Firehole River watershed (Despain 1973). The total fire frequency, including both small and major fires, was five times greater in the Two Ocean and Mirror Plateau study area than in the Little Firehole River watershed (Table 6). This is to be expected since many prehistoric small fires in the Little Firehole River watershed undoubtedly left no scarred trees or other evidence. The record for major fires in the Little Firehole River watershed is more complete, but again the frequency of major fires has been two to three times greater on the Two Ocean and Mirror Plateaus (Table 6). These comparisons must be made with some caution, since the Two Ocean and Mirror Plateau study area is nearly 20 times larger than the Little Firehole River watershed (Table 6). Given that 30 fires occurred in a 1380-km² area during a 7-yr period, it does not necessarily follow that a 69-km² portion of that larger area ($1/20$ of the total area) experienced 1.5 fires ($1/20$ of the total number of fires), as Table 6 implies. Total fire frequency in the Pico/Cage habitat type in the Little Firehole River watershed has been nearly twice that in the Abia/Vasc habitat type but the frequency of major fires has been approximately equal in the two habitat types (Table 6).

Fig. 2 shows the sizes of all documented major fires since 1600 in the Pico/Cage habitat type, Abia/Vasc habitat type, and the entire Little Firehole River watershed. The areas are expressed as percent of total area rather than square kilometres because several fires also burned adjacent areas outside the watershed, and their total size is unknown. Although the frequen-

TABLE 5. Fire years since 1600 in the 73-km² Little Firehole River watershed. Major fires burned >4 ha, destroyed the existing forest, and initiated secondary succession.

Fire year	Major fire	Pico/Cage* habitat type	Abla/Vasc† habitat type	Fire scar sample dates
1949	X		X	1949, 1949, 1949, 1949, 1949
≈1932		X		≈1932
1905	X		X	1905, 1907, ≈1912
≈1890		X		≈1888, ≈1889
≈1881			X	≈1881
≈1860		X		≈1858, ≈1859
≈1851			X	≈1851
1834	X	X		1834
≈1827		X		≈1827
1795	X	X	X	1792, 1793, 1794, 1794, 1795, 1795, 1795, 1795, 1795, 1795, 1795, 1795, 1796, 1797, 1797, 1797, 1797, 1797, 1797, 1798, 1798, ≈1802
1755	X		X	1755
1739	X	X	X	1739, 1739, 1739, 1739, 1740, 1741, 1741, 1742, 1742, 1743, 1743, 1744, ≈1746
≈1659		X		≈1659
≈1643		X		≈1643
≈1630	X	X	X	‡

* *Pinus contorta*/*Carex geyeri* habitat type.† *Abies lasiocarpa*/*Vaccinium scoparium* habitat type.

‡ Evidenced by extensive 350-yr-old lodgepole pine forests.

cy of major fires has been approximately equal in the two upland forest habitat types (Table 6), over 90% of the area in the Pico/Cage habitat type has burned, compared to only 55% of the area in the Abla/Vasc habitat type (Fig. 2). This difference may partly reflect the greater precipitation in the western and southern portions of the watershed where the Abla/Vasc habitat type is found. In addition, there are several topographically sheltered sites in this area that probably rarely burn. A climax spruce-fir forest, containing spruce and pine >500 yr old and no evidence of fire, covers ≈1.5 km² on a northeast-facing slope that is protected from the prevailing southwest wind and contains numerous springs and seeps.

Several kinds of evidence indicate that fires covering large areas in the Little Firehole River watershed were chiefly destructive, stand-replacing burns. The extensive, low-intensity, nonstand-replacing burns reported for subalpine forests in the northern Rocky

Mountains (Arno 1980) apparently are of minor importance here. This interpretation is supported by the fact that fire-scarred trees in my study area are usually found in clumps and rarely have more than a single fire scar, indicating that they represent the margins of destructive burns or islands of unburned trees within a burned area. Furthermore, most lodgepole pine stands are dominated by a single age-class. Finally, as discussed below, analysis of the fuel complex indicated a low probability of extensive, low-intensity surface fires, and recent, uncontrolled burns in the Park have been observed to cover large areas only when they entered the canopy (Sellers and Despain 1976, D. G. Despain, *personal communication*). Only a very small portion of the watershed (<10%) has burned more than once during the last 350 yr, mainly along boundaries between two burns where the second fire apparently burned a short distance into the area burned earlier before going out.

TABLE 6. Historical fire frequencies in the Little Firehole River watershed (data from this study) and on the Two Ocean and Mirror Plateaus, Yellowstone National Park (data from Sellers and Despain 1976, and D. G. Despain, *personal communication*). Major fires burned >4 ha, destroyed the existing forest, and initiated secondary succession.

	Area (km ²)	All fires		Major fires		Fire frequency (fires · 100 km ⁻² · yr ⁻¹)	
		Time period	Number of fires	Time period	Number of fires	All fires	Major fires
Little Firehole River watershed							
Pico/Cage habitat type	25.4	1630–1932	10	1630–1834	4	0.117	0.058
Abla/Vasc habitat type	36.1	1630–1949	8	1630–1949	6	0.061	0.043
Entire watershed	73.2	1630–1949	15	1630–1949	7	0.060	0.026
Two Ocean and Mirror Plateaus							
	1380	1972–1978	30	1972–1978	7	0.311	0.072

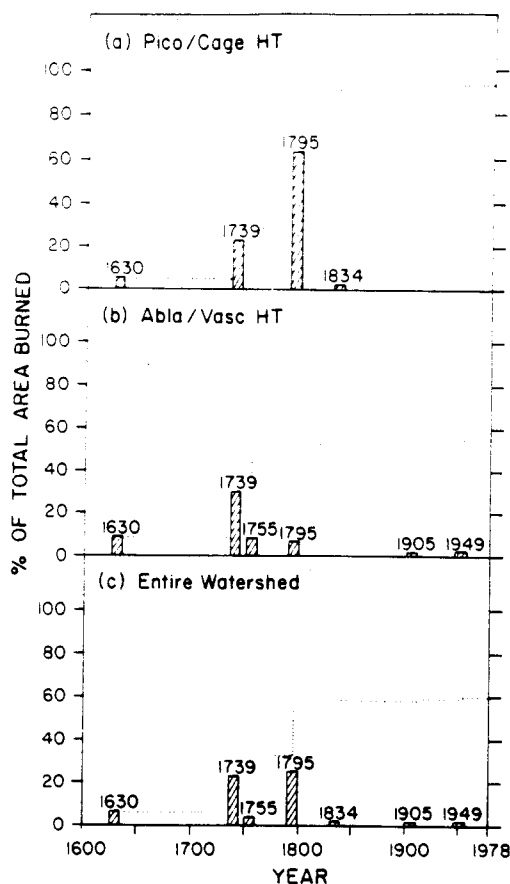


FIG. 2. Sizes of documented major fires since 1600 in the Pico/Cage habitat type (HT), Abia/Vasc HT, and entire Little Firehole River watershed, expressed as percent of total area in the habitat type or the watershed. The dotted line shows the cumulative area burned since 1600.

Fuel accumulation

Quantities of small fuels capable of supporting fire ignition and initial spread (needle litter and 1-h TL; Table 2) are low in early successional stages but increase to a maximum at 150–200 yr due to litterfall, self-pruning, and suppression mortality in the maturing, even-aged pine forest (Fig. 3). The amount of needle litter remains constant, and 1-h TL fuels decrease slightly in later stages as production of small materials declines and is balanced by decomposition. The regression lines in this and subsequent figures are included primarily to indicate periods where fuel changes are significant ($P < .1$); a larger data base would be necessary for rigorous predictive models (cf. Bevens et al. 1977). The small quantity of readily ignitable fine fuels during the first 100 yr of stand development probably precludes extensive fires during early successional stages. Even in later stages the fine fuels apparently are not adequate to support a fast-moving surface fire. Using my data for 350-yr-old and 450-yr-old stands in the Little Firehole River wa-

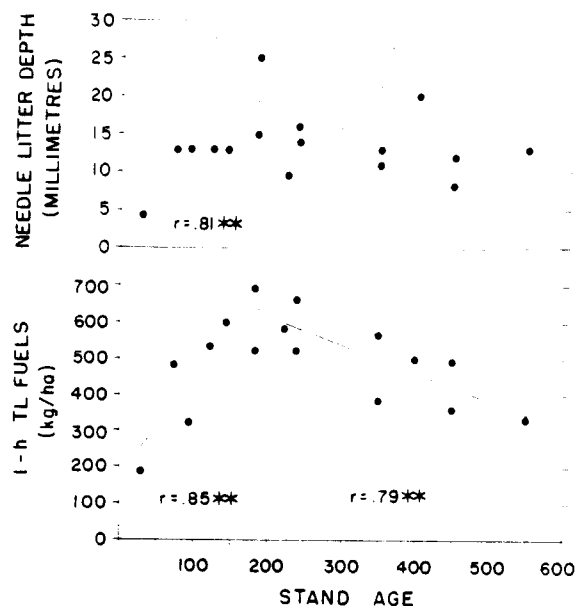


FIG. 3. Changes in small fuels capable of supporting ignition and initial fire spread along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero ($** P < .05$).

tershed, Rothermel's (1972) fire model predicted low spread rates and intensities even under high wind and low moisture conditions, with maximum expected values of 3.0–3.6 m/min and 250–360 $J \cdot s^{-1} \cdot m^{-1}$ of fire-line, respectively (Romme 1979: Appendix 2). These values are in the same range as values reported for controlled, prescribed fires (Byram 1959, Norum 1976).

The total mass of dead, woody fuels is high immediately after a major fire, consisting mainly of large fire-killed stems (Fig. 4). The developing even-aged pine forest contributes primarily small fuels during the first 200 yr of succession, and decomposition of large fire-killed material results in a net decline in total fuels to a minimum between ≈ 70 and 200 yr. Total fuels then begin to increase with the onset of extensive mortality in the even-aged canopy, reaching a peak around 350 yr. Although potential heat release in a fire is a function of the total fuel mass present (Byram 1959), generally only the rotten wood and the sound material up to ≈ 7.5 -cm diameter actually burn during intense fires in Yellowstone National Park (D. G. Despain, *personal communication*). However, the larger sound material (1000-h TL fuel) that does not burn completely constitutes a major portion of the total fuel mass in stands > 200 yr old. Therefore, I also examined changes in total fuels (i.e., all rotten material plus sound pieces < 7.5 -cm diameter) excluding the relatively noncombustible 1000-h TL sound fuels and observed the same general pattern except that maximum fuel accumulations occur later, around 450 yr (Fig. 4).

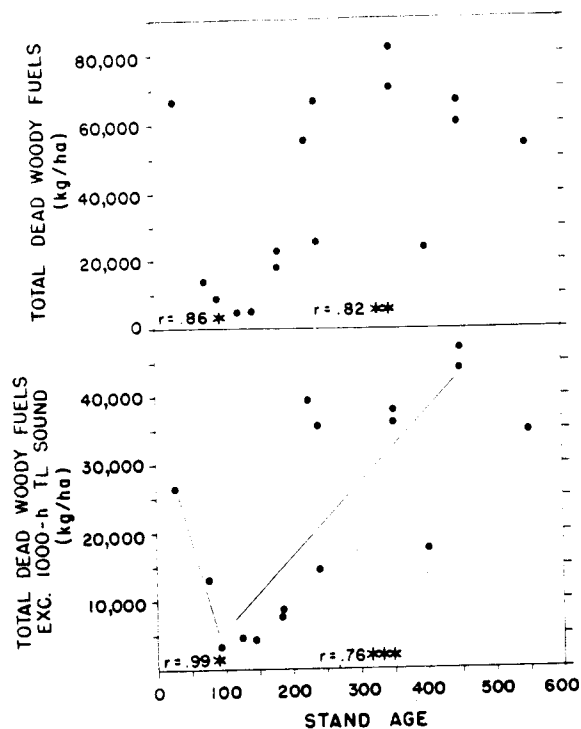


FIG. 4. Changes in total dead woody fuels and in total fuels excluding 1000-h TL sound fuels along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero (* $P < .1$, ** $P < .05$, *** $P < .01$).

An important factor controlling initiation of a crown fire is the distance or vertical continuity between the surface fire and the canopy. With increasing distance the minimum surface fire intensity required to raise the canopy temperature above a critical ignition point also increases. A crown fire occurs more readily where the surface fuel bed is adjacent to and continuous with the canopy fuels (Van Wagner 1977). The changes in canopy continuity through succession shown in Fig. 5 are based on qualitative observations. Vertical continuity is high in very young stands where the small trees have living branches close to the ground, although fire is unlikely at this stage because of the small amount of fine fuels present. Subsequent self-pruning by maturing lodgepole pine eventually creates a gap between the lowest branches and the ground. In a mature pine forest (≈ 200 yr old) this space may be 3 m or more and filled only by relatively nonflammable large tree trunks. At about the time the even-aged lodgepole pine forest begins to break up with natural mortality (≈ 250 – 300 yr), a well-developed understory also begins to appear, producing a gradual increase in vertical fuel continuity as the saplings grow into the canopy. Spruce and fir saplings, which retain their lower branches throughout their lives, create greater vertical continuity than small lodgepole (*Pinus con-*

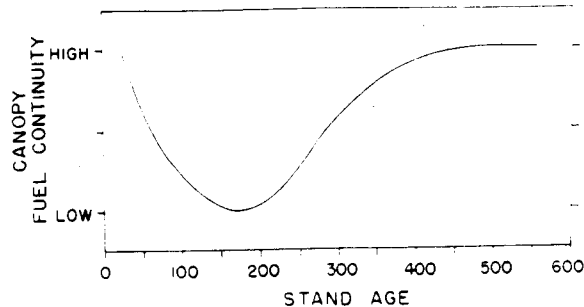


FIG. 5. Qualitative changes in total canopy fuel continuity (a composite of vertical and horizontal continuity) along a chronosequence of upland forest stands.

torta) and whitebark pine (*P. albicaulis*), which shed lower branches as they grow. Once a fire reaches the canopy, horizontal canopy continuity or the distance between tree crowns influences the probability that it will move through the canopy (Van Wagner 1977). During the stage of extensive mortality in the even-aged lodgepole pine forest (≈ 250 – 300 yr), a visual impression is that the canopy is too sparse to sustain a moving crown fire, even though the developing understory may create sufficient vertical continuity to carry the fire into individual tree crowns. With maturation of the understory (≈ 400 yr), however, both vertical and horizontal canopy continuity appear adequate to support an intense crown fire (Fig. 5).

Quantities of fuels in which a fire may smolder and persist during cool, humid, or rainy periods (1000-h TL rotten fuels and duff) are generally low during early and middle successional stages but increase in later

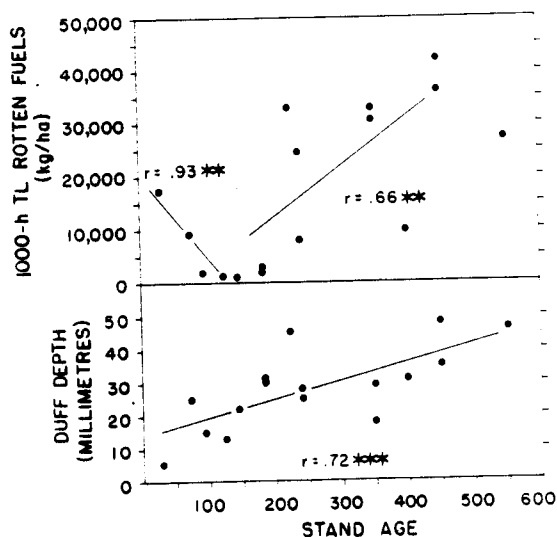


FIG. 6. Changes in fuels in which a fire may persist during periods of unfavorable weather along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero (** $P < .05$, *** $P < .01$).

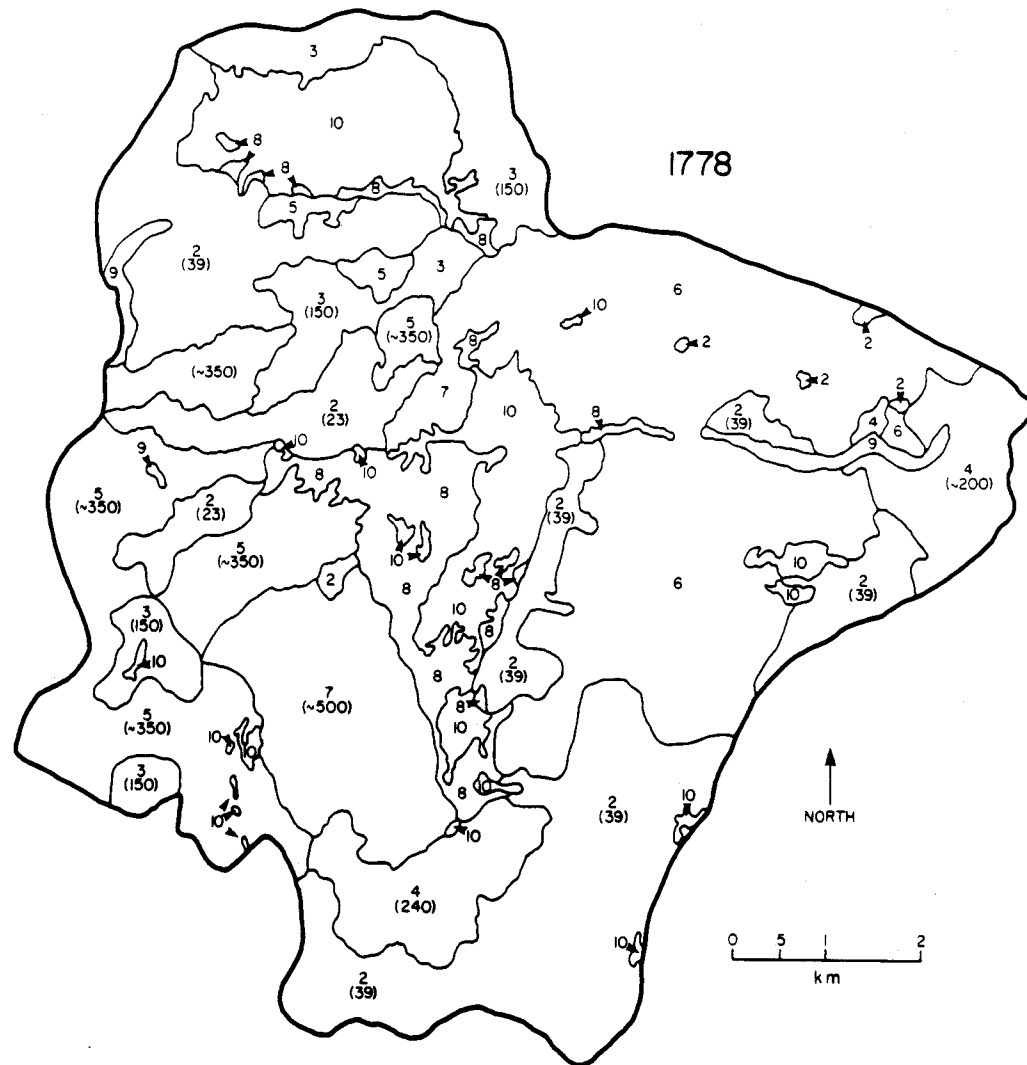


FIG. 7. Reconstruction of community types and stand ages (in parentheses) in the Little Firehole River watershed in 1778. The precise stand age could not be estimated in areas that were later burned. However, evidence indicates that these areas must have been in climax forest stages when they burned (see text). Community types are defined in Table 1 and are described in the section, Study Area.

stages (Fig. 6). This may be important because many recent uncontrolled fires in Yellowstone National Park have been observed to persist for weeks or months before being extinguished by heavy rain or snow (Sellers and Despain 1976, Despain and Sellers 1977). During most of that time, the fire smoldered at low intensity in duff and rotten wood, flaring up periodically when weather conditions became favorable (warm, dry, and windy). Such a fire might flare up two or more times during a summer, burning a large area on each occasion.

In addition to the patterns based on sample means shown in Figs. 3-6, sample variance (s^2) in 20 transects increased significantly ($P < .10$) with increasing stand age for 1-h TL fuels, needle litter depth, 1000-h TL rotten fuels, and duff depth (Romme 1979: Appen-

dix 2). This supports Despain and Sellers' (1977) qualitative observation that the fine fuels supporting ignition and initial spread become distributed less homogeneously in older stands, as do the fuels that allow a fire to persist during unfavorable weather. This results in local patches where the fuel accumulation is unusually high, interspersed with areas having relatively sparse fuels. These high-fuel patches are probably important for generating sufficient heat to ignite tree crowns and larger dead fuels as well as for sustaining smoldering fires (Despain and Sellers 1977).

Needle litter depth is negatively correlated with site index in stands 200-600 yr old ($r = -.77$, $P < .025$; Romme 1979: Appendix 2), possibly reflecting more rapid litter turnover on more productive sites. This relationship is somewhat tentative, however, because

as noted in the Methods section, site index could not be measured directly in stands >200 yr old, and some of the estimates may be in error. Otherwise I found no correlations with $P < .1$ between site index and fuel accumulation.

Long-term patterns in landscape diversity

I began the simulations on landscape reconstruction data with the year 1778 (Fig. 7) and determined how today's landscape might differ if 20th-century man had entered the Yellowstone region 200 yr earlier. I compared three scenarios: (1) natural fire, based on the fires that actually occurred in the last 200 yr, (2) total fire exclusion, and (3) selective fire control, in which only small fires (covering <5% of the watershed) were allowed to burn. Between 1778 and 1978 there were four major fires under the natural fire regime, zero under total fire exclusion, and three under selective fire control.

I first examined changes in the proportion of the watershed covered by early, middle, and late successional stages under the three fire regimes, combining the Pico/Cage and Abia/Vasc habitat types for this analysis. Early stages include the period of tree reestablishment immediately following a destructive fire (community types 1 and 2, Table 1; stand age 0 to ≈ 40 yr); middle stages are characterized by maturation of the even-aged lodgepole pine forest that initially dominates a site (types 3 and 4; age ≈ 40 to ≈ 250 yr); and late stages include the progressive deterioration of the even-aged pine canopy, with replacement by climax species (types 5, 6, and 7; age $\approx 250+$ yr). Meadows, riparian forests, and steep-slope forests, which together cover 16% of the watershed, were assumed to have remained constant.

Fig. 8 shows a 240-yr simulation of landscape changes under three different fire regimes. The selective fire control and total fire exclusion hypothetical policies were in effect from 1778 to 1978 in the simulations. In 1738 the watershed was dominated by late successional forests, with only small areas covered by early and middle stages. Under the natural fire regime (Fig. 8a) the old-growth forests were greatly reduced by major fires in 1739, 1755, and 1795, and large areas of early successional stages were created. After 1818 the area covered by early successional stages declined steadily and has remained very low (<5%) since the mid-1800's, a result of succession on the earlier burned areas and the absence of large fires during the last 180 yr. The area covered by middle successional stages increased dramatically around 1800, and these stages still dominate the watershed today. Middle successional stages have begun to decrease during the last half century, with a concurrent increase in late successional stages as areas burned in 1739 begin to enter the more mature developmental stages.

Had a selective fire control policy been in effect

after 1778 (Fig. 8b), the fire in 1795 would have been excluded, and late successional stages would have dominated the watershed throughout the last 240 yr. Middle stages would have reached an earlier, lower peak than occurred naturally, and early successional stages would have declined rapidly in the late 1700's, leveling out sooner at the same low level reached under a natural fire regime. The simulation for total fire exclusion (Fig. 8c) shows patterns similar to selective fire control except that early successional stages are absent after 1800.

Fig. 9 shows changes in the area covered by early, middle, and late successional stages in the Pico/Cage and Abia/Vasc habitat types under a natural fire regime. Major patterns are similar in the two habitat types except that changes in the Abia/Vasc habitat type occur 40–50 yr earlier than corresponding changes in the Pico/Cage habitat type. This is because the large fire in 1739 burned primarily in the Abia/Vasc habitat type, whereas in 1795 mainly the Pico/Cage habitat type was affected. These two large fires each produced a dramatic but relatively short-lived increase in the area covered by early successional stages, followed by a prolonged increase in middle successional stages.

Fig. 10 shows long-term patterns in landscape diversity indices based on 10 community types (Table 1). Changes in the richness index (Fig. 10a) primarily reflect the appearance and disappearance of two short-lived early successional stages that follow major fires (community types 1 and 2). Richness was highest under the natural fire regime in the early 1800's when all 10 community types were present. Richness declined thereafter, and reached a low point in the late 1800's during a 70-yr period when no major fires occurred and both early successional stages disappeared from the landscape. Fires in 1905 and 1949 have increased richness during the 20th century. Had the 1795 fire been excluded under a selective fire control policy (Fig. 10a), richness in the early 19th century would have been much lower than occurred naturally. After about 1850, however, richness would have been equal under the natural fire and selective fire control policies since the same small fires would have occurred with both. Total fire exclusion since 1778 would have produced a slow, steady decline in richness as the two early successional stages and eventually also the first middle successional stage (community type 3) disappeared from the watershed (Fig. 10a).

Landscape evenness under the natural fire regime was relatively high around 1800, but it declined sharply between 1818 and 1838 and remained low until the end of the 19th century (Fig. 10b). During that time, 40–50% of the watershed was covered by a single community type, namely immature pine forests that had developed after the extensive fires of 1739 and 1795. By 1900 the forests on most of the area burned in 1739 had progressed to the mature pine forest stage; the

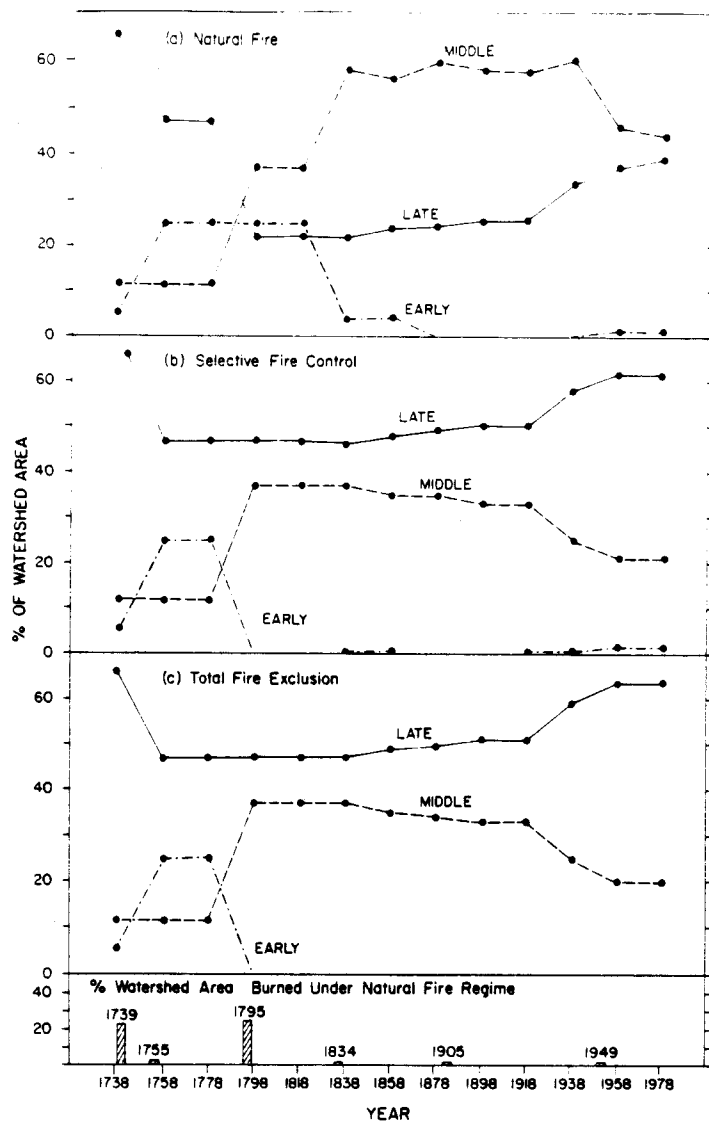


FIG. 8. Percent of area in the Little Firehole River watershed covered by early, middle, and late forest successional stages since 1738 under three different simulated fire regimes: (a) natural fire—all fires allowed to burn, (b) selective fire control—large fires excluded, small fires allowed to burn, and (c) total fire exclusion. In (b) and (c), fire control begins in 1778.

watershed area was now more evenly distributed among community types, and the evenness index increased (Fig. 10b). Evenness declined again after 1938 and has remained low because most of the forests developing after 1795 have now also reached the mature pine forest stage, resulting once more in a preponderance of one community type (Fig. 10b). Had the large 1795 fire been excluded under a selective fire control policy, the relative proportions of forest successional stages during the 19th and 20th centuries would have been more uniform, and landscape evenness would have been greater (Fig. 10b). The highest evenness values would have occurred with total fire exclusion (Fig. 10b). This is because fires after 1800 created

small patches of early successional stages within a landscape dominated by middle and late successional stages, resulting in an uneven distribution of area among community types.

Landscape patchiness under a natural fire regime was highest in the late 1700's and early 1800's, following fires in 1739, 1755, and 1795 (Fig. 10c). Patchiness declined after 1818 and remained low until the period 1938–1958 when it again increased. This recent increase has occurred partly because of small fires in 1905 and 1949, but also because of extensive local variation in the rate of succession and in the onset of extensive canopy mortality in even-aged pine forests on the areas burned in 1795 in the Pico/Cage habitat

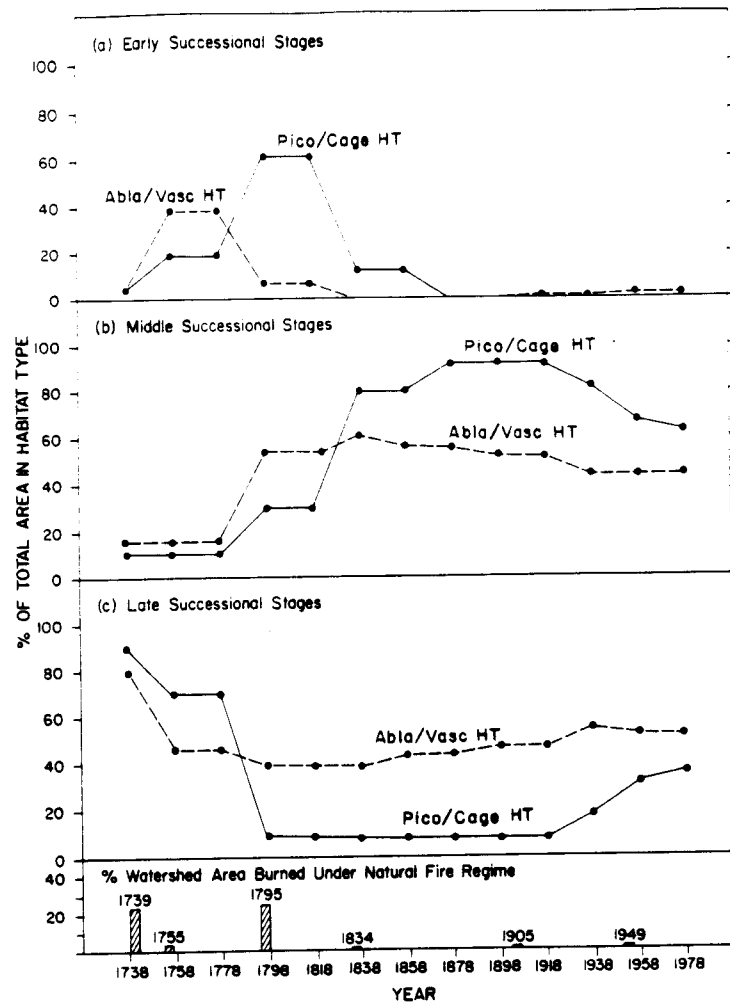


FIG. 9. Percent of area in the Pico/Cage and Abia/Vasc habitat types (HT) covered by early, middle, and late forest successional stages since 1738 under a natural fire regime.

type. Had the 1795 fire been excluded under the selective fire control policy, landscape patchiness would have decreased sharply after 1778 and remained low thereafter except for a much smaller increase between 1938 and 1958 (Fig. 10c). With total fire exclusion, landscape patchiness would have continued to decline into the 20th century.

Fig. 11 shows long-term patterns in overall landscape diversity. A weighted average of relative richness, evenness, and patchiness (Fig. 11a) and the Shannon-Wiener Index (H' ; Fig. 11b) show similar patterns. Landscape diversity under the natural fire regime was highest in the early 1800's, fell to a low level in the mid-1800's, then increased again in the late 1800's. Overall diversity under selective or total fire control would have been lower in the early 1800's, but would have been substantially higher in the mid-1800's than occurred naturally. This latter result seems sur-

prising, because fire is generally regarded as an event that increases diversity in coniferous ecosystems. However, when the forests developing on areas burned in 1795 entered the middle successional stage (community type 3), which was already widespread following the major fire of 1739, evenness declined so much that the overall diversity indices (which contain an evenness component) were also lowered. Such a reduction in landscape diversity does not necessarily occur after every major fire. The earlier large fire of 1739 probably increased richness, evenness, and patchiness for several decades; overall diversity was still high in 1778 (Fig. 11), some 40 yr after the fire, and it declined only slowly after 1778 in the simulations that excluded the fire in 1795. In contrast to the fire of 1795, the fire of 1739 occurred after a long, relatively fire-free period, in a landscape dominated by late-successional communities (Fig. 8a). Fig. 11

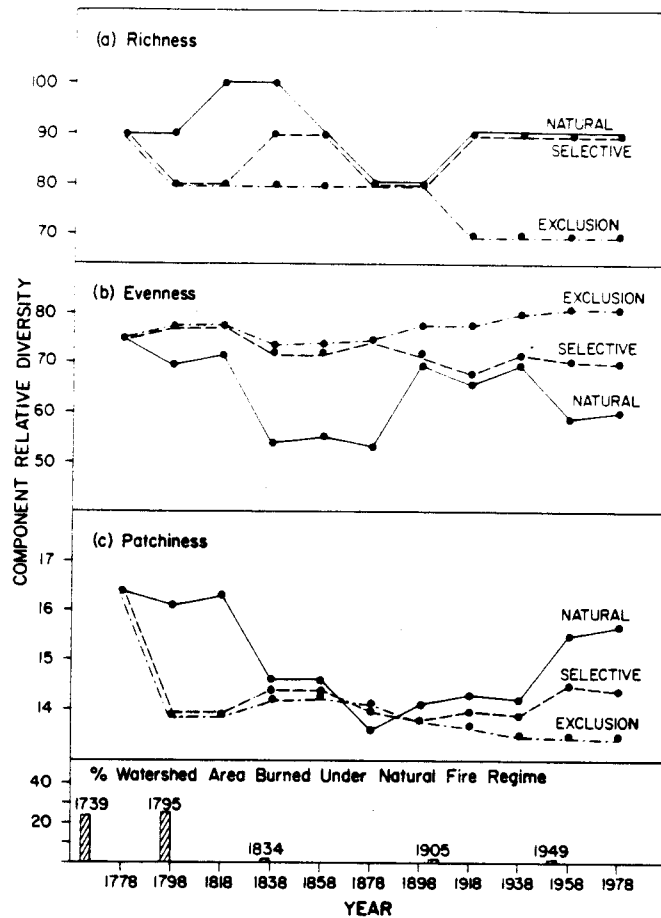


FIG. 10. Relative richness, relative evenness, and relative patchiness in the Little Firehole River watershed since 1778 under three different simulated fire regimes: (a) natural fire—all fires allowed to burn, (b) selective fire control—large fires excluded, small fires allowed to burn, and (c) total fire exclusion.

also shows that overall landscape diversity has changed little during the actual period of fire suppression in the 20th century.

DISCUSSION

Fire cycles in subalpine forests of Yellowstone National Park

The fuels data in Figs. 3–6 support Despain and Sellers' (1977) hypothesis that the frequency of major fires in this area is partly controlled by the slow development during succession of a fuel complex capable of supporting an intense crown fire. Surface fires of low intensity do occur, but because even the maximum accumulations of fine fuels are relatively low (Fig. 3) and because the small needles tend to form a compact litter layer, light surface fires generally spread slowly and cover only small areas. Thus they exert a minor influence on long-term vegetation structure and dynamics compared to the dramatic effects of crown fires, which may burn very large areas and produce major vegetational changes.

After a suitable fuel complex has developed in a stand, with adequate quantities of all fuel components necessary to support a crown fire (stand age 300+ yr; Figs. 3–6), a destructive fire is likely to occur if lightning ignites small fuels during warm, dry, windy weather. Such weather conditions occur every summer in this area, and lightning-caused fires have been reported in Yellowstone Park in every year for which records have been kept (Sellers and Despain 1976). However, these fires are widely scattered over the Park, and any particular stand may escape fire for many years, even though it has suitable fuel conditions. Therefore, I concluded that the mean fire interval, or length of time between two successive crown fires in a small stand of a few hectares or less, must be a minimum of 300–350 yr, the average time necessary for the fuel complex to develop, but it may be much longer.

Over half of the upland forest area in the Little Firehole River watershed was burned by three major fires in the 18th century (1739, 1755, 1795; Fig. 2).

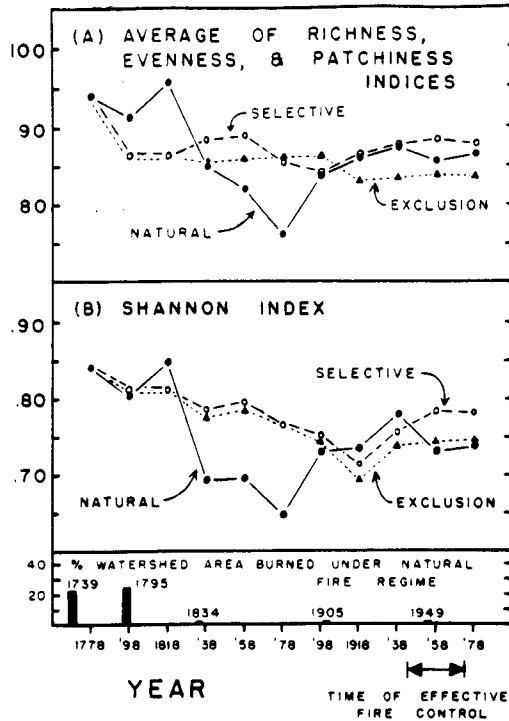


FIG. 11. Overall landscape diversity in the Little Firehole River watershed since 1778, expressed as: (A) a weighted average of the relative richness, relative evenness, and relative patchiness indices, and (B) the Shannon (Shannon-Wiener) Index (H').

Most of the area that escaped burning at that time either was sheltered topographically or had been burned by the fire of 1630, <200 yr earlier. As a result, most of the upland forest today is in middle stages of succession (Fig. 8), with low quantities of most fuel components and a low probability of crown fire developing even if ignition occurs (Figs. 3–6). This probably explains the low frequency and small size of fires in the watershed during the last 180 yr (Fig. 2). In another 150–200 yr, most of these forests will have entered late successional stages in which the probability of crown fire is high if ignition occurs. This fact, plus the scarcity of topographic barriers to fire spread in the watershed, leads me to predict that another series of large, destructive fires will again burn most of the upland area in 150–200 yr. Thus, this ecosystem appears to be characterized by a long-term fire cycle in which extensive areas burn every 300–400 yr, with relatively few major fires during the intervening periods.

A 300-yr fire cycle may help to explain why the frequency of major fires since 1972 on the Two Ocean and Mirror Plateaus in eastern Yellowstone Park has been twice as great as the frequency during the last 300 yr in the Little Firehole River watershed (Table 6). The latter area is now in a prolonged phase of the cycle where major fires are unlikely because of the

vegetational composition of the landscape. On the much larger Two Ocean and Mirror Plateaus, however, there probably are areas in a different phase of the cycle in which major fires are more likely to occur. Another possible explanation for the difference in fire frequency is that weather conditions conducive to a major fire have occurred more frequently during the last 6 yr than occurred on the average over the last 350 yr. However, this latter explanation seems unlikely. Even if recent weather patterns may have been drier and warmer, fires in the past could have covered very large areas even during a single short period of favorable weather if a suitable fuel complex had been present (Sellers and Despain 1976).

Detailed fire history studies in other parts of the Rocky Mountain subalpine zone suggest that there is some geographic variation in fire frequency. Clagg (1975) reported an average of 7.12 lightning fires·million acres⁻¹·yr⁻¹ in areas above 2575 m in Rocky Mountain National Park in northern Colorado, USA, and estimated that 0.5 fires larger than 10 acres occurred per million acres per year prior to 1870. Conversion of these data to metric units yields a frequency of 0.18 fires·100 km⁻²·yr⁻¹ for all fires and 0.012 fires·100 km⁻²·yr⁻¹ for major fires. The frequency of major fires appears to be substantially higher in Yellowstone National Park, with 0.026 fires·100 km⁻²·yr⁻¹ determined for the Little Firehole River watershed and 0.072 fires·100 km⁻²·yr⁻¹ determined for the Two Ocean and Mirror Plateaus (Table 6). Total fire frequency also is higher on the Two Ocean and Mirror Plateaus, with 0.31 fires·100 km⁻²·yr⁻¹ (Table 6). I did not compare total fire frequency in my study area because, as noted earlier, the record of very small fires here is almost certainly incomplete. A comparatively lower fire frequency in the Colorado mountains may be due to greater summer precipitation; Clagg (1975) reports that fuel moisture is usually high throughout the summer due to frequent rain showers.

There is also considerable variation in mean fire intervals in different parts of the Rocky Mountain subalpine zone. Arno (1980) has summarized the results of several recent, detailed fire history studies in the Northern Rocky Mountains (Alberta, Montana, and Idaho), which report mean intervals ranging from 22 to 153 yr between successive fires in small stands (≈40 ha). My estimate of 300 yr for the Yellowstone subalpine zone is substantially longer than any of these other estimates. I believe that there are two major reasons for this, one related to differences in methods and types of fires being considered, and the other reflecting a significant difference in fuel dynamics and fire behavior in the various study areas. With respect to methods, estimates summarized by Arno (1980) were obtained by listing all fire years detected in small stands and calculating the average interval between fire years in each stand. Many of the fires detected in these areas were of relatively low intensity; they nei-

ther killed all of the canopy trees, nor consumed all of the dead woody fuels. Such light surface fires apparently have been much more frequent and covered larger areas in subalpine forests of the Northern Rockies than in Yellowstone; hence the mean fire intervals in the Northern Rockies are shorter. By consuming a significant portion of the accumulated fuel, these fires may delay the occurrence of destructive crown fires (Gabriel 1976).

The method just described could not be used in my study area where very few stands contain evidence of more than one fire. The few stands that do show evidence of two fires appear to represent either (1) the boundaries between two large burns where the second fire burned a short distance into the area burned earlier before going out, or (2) the site of a very small, localized fire that left no evidence of its presence other than one or a few fire-scarred trees. Had I calculated mean fire intervals in these stands I would have obtained estimates of 32–183 yr, but these results would not be representative of the study area as a whole. Therefore, I determined a minimum likely fire interval on more typical sites based on the time required for development of a suitable fuel complex. I emphasize that my estimate of 300+ yr applies to the average interval between major crown fires that destroy a stand and initiate secondary succession. Fires of lower intensity do occur, but they are usually very small and have a minimal impact on the overall vegetation pattern of the Yellowstone subalpine zone.

Despite differences in method and in types of fires included in calculations, there seem to be some very real differences in the mean fire intervals of subalpine forests in Yellowstone and in the Northern Rockies. Most of the Yellowstone Plateau lies at relatively high elevations (≈ 2500 m) and has comparatively poor growing conditions (100-yr site index 50–60 feet [15–18 m] in my study area). On more productive sites at lower elevations, tree growth and fuel accumulation probably occur more rapidly between fires, making more frequent fires possible (Arno 1980). The mountain pine beetle (*Dendroctonus ponderosae*), which hastens succession and fuel accumulation, is also more abundant at lower elevations (Amman et al. 1977). Within the study areas referred to by Arno (1980), mean fire intervals generally become longer as elevation increases. Even in the areas surrounding Yellowstone National Park there appear to be significant differences in mean fire intervals related to elevation and soil type. A fuel complex capable of supporting a destructive crown fire apparently can develop in as little as 100 yr in lodgepole pine (*Pinus contorta*) forests on the floor of Jackson Hole, Wyoming, USA, ≈ 80 km south of the Yellowstone Plateau, and 500 m lower in elevation. A major fire there in August 1981, burned intensely in a 100-yr-old forest that had been affected by a severe outbreak of mountain pine beetles 20 yr earlier. I observed that the understory and fuel con-

ditions in this forest resembled those of a 300-yr-old stand on the Yellowstone Plateau, apparently due to more favorable growing conditions and significant insect-caused mortality in the canopy of the younger stand. In contrast, lodgepole pine forests growing on poor soils at high elevations in the Wind River Mountains (≈ 100 km southeast of Yellowstone) contain little evidence of fire, and fuel accumulation appears very slow (Arno 1980); the fire regime there is probably similar to that on the Yellowstone Plateau.

Quantitative data on fuel accumulation in relation to stand age from other Rocky Mountain subalpine forests support the idea that development of the fuel complex occurs more slowly in Yellowstone Park than in some other areas, although relatively few comparable data are available. Bevins et al. (1977), using data from a large area in southwestern Montana, obtained patterns very similar to those in Figs. 3–6 except that major changes in fuel quantities generally occurred 50–100 yr earlier. Clagg (1975) observed somewhat different patterns in lodgepole pine forests of Rocky Mountain National Park. There the duff plus litter layer increases to a maximum between ages 100 and 200 yr and then declines steadily, in contrast to the pattern in Yellowstone National Park (Figs. 3, 6) in which these components also reach high levels at 100–200 yr but then remain high or continue to increase. Clagg found that total dead woody fuels increase immediately after a fire, quickly decline to a low point at about age 50 yr, then rapidly increase again to a peak at 100 yr, followed by a gradual decline until about age 300 yr, after which fuel mass appears to remain constant. In contrast, Fig. 4 for Yellowstone National Park shows a low point for total fuels around age 70–200 yr, followed by a slow increase to maximum levels around 350 yr. Clagg also noted that fine fuels are not very abundant and generally discontinuous, a situation similar to that in Yellowstone. Muraro (1971) was unable to recognize any clear patterns of fuel accumulation in relation to stand age in lodgepole pine forests of British Columbia, concluding that stand history and the intensity of previous fires were the major controlling factors.

Long-term patterns in ecosystem structure, function, and diversity

A striking result of my 200-yr landscape reconstruction is that landscape composition and diversity in the Little Firehole River watershed have fluctuated greatly under a natural fire regime (Figs. 8a, 10, 11). These results lead to the conclusion that the vegetation of this watershed has not been in a steady-state condition during the last 200 yr. Moreover, if the area is subject to a cycle of extensive fires every 300 yr, as described earlier, then this particular landscape must be characterized over the long term by continual change. Loucks (1970) referred to similar long-term dynamics in individual communities as a "stationary process

with random perturbation." Loucks pointed out that a community at any particular time may appear "unstable" because its composition is changing, but that the entire long-term sequence of changes actually constitutes a "stable" system because the same sequence recurs after every interruption by fire or other perturbations. Botkin and Sobel (1975) also referred to this type of recurrence as an important form of stability in ecosystems. The 73-km² Little Firehole River watershed appears to represent a similar stationary process of much greater size and complexity. One important difference here is that perturbation, rather than being random as Loucks indicated, is actually highly predictable because of changes in fire susceptibility during community development (cf. Mutch 1970). Rowe (1961) suggested a similar interpretation for the Canadian western boreal forest, calling it a "disturbance forest" maintained by frequent fires to which nearly all species are well adapted.

Although the Little Firehole River watershed clearly is not characterized by steady-state conditions, we can speculate whether the idea of steady state may apply at some higher level of ecological organization, perhaps encompassing the entire subalpine portion of the Yellowstone Plateau. One could hypothesize that while early successional communities have become scarce in the Little Firehole River watershed during the last 180 yr, fires in other watersheds have continually re-created them, so that the proportion of this very large area covered by early successional stages has remained relatively constant over time. Several authors have suggested this kind of dynamic equilibrium in landscapes (White 1979). Zackrisson (1977) indicated that the spatial distribution of postfire successions in the North Swedish boreal forest is always changing, but over the long term the forest mosaic in the region as a whole remains unchanged. Studies of wave-regenerated fir forests in the northeastern United States have indicated that the entire fir forest ecosystem is in a steady-state condition despite widespread local patterns of community degradation and regeneration (Sprugel 1976, Sprugel and Bormann 1981). Similarly, Bormann and Likens (1979) concluded that, prior to European settlement, the northern hardwood forests of the White Mountains in New Hampshire were characterized by a "shifting-mosaic steady state" in which the standing crop biomass of a watershed or other large landscape unit varied slightly around a mean, although the biomass on any small plot within that unit fluctuated greatly over time due to localized disturbance by treefalls and subsequent forest regrowth.

If such a steady state exists in the Yellowstone subalpine ecosystem, it must be on a very large scale, encompassing an area much greater than one 73-km² watershed, due to the very large scale of fire-induced disturbance. For the purposes of management and in-

terpretation of natural phenomena in the Park (e.g., patterns in wildlife populations), I suggest that this particular ecosystem is more appropriately viewed as a nonsteady-state system characterized by cyclic, long-term changes in structure and function brought about by periodic large, destructive fires. Note that fire controls landscape dynamics in Yellowstone not because it recurs very frequently, but because very large areas are affected when it does occur, and vegetational development between fires is relatively slow.

Concurrent with the changes in overall vegetational composition and landscape diversity shown in Figs. 8–11, there must have been changes in functional characteristics of the Little Firehole River watershed ecosystem. For example, removal of forest cover from large portions of a subalpine watershed by fire or logging often leads to a significant increase in streamflow (Leaf 1975, Albin 1979) and at least a brief increase in nutrient output in stream water (Likens et al. 1970, McColl and Grigal 1975, Wright 1976). Long-term hydrologic and nutrient-cycling patterns in relation to fire are poorly understood in the Yellowstone ecosystem, but they may have important bearing on the structure and productivity of aquatic as well as terrestrial ecosystems. Of particular interest are the large subalpine lakes in Yellowstone Park in which total productivity and carrying capacity for fish appear to have declined during the last century (Varley 1974, Shero 1977). Cyclic patterns in landscape composition and diversity are also important in interpreting long-term population dynamics of terrestrial animal species that require or prefer habitats in particular forest successional stages. Taylor (1969, 1973, 1974) found a larger number of species associated with early forest successional stages than with middle or late successional stages in subalpine forests of Yellowstone Park. There is much less area covered by early successional stages today than there was 150 yr ago in the Little Firehole River watershed; consequently the populations of many animal species undoubtedly have declined since that time, while populations of a few species have increased. Some population fluctuations in the Park as a whole may be the result of natural landscape changes rather than the influence of man.

Management implications

All evidence indicates that normal landscape dynamics in the Little Firehole River watershed have not been significantly interrupted by human activities. The former policy of total fire exclusion occurred at a time when large fires in this area were unlikely anyway. In fact, the one fire that was suppressed in 1949 probably would not have been much larger if left uncontrolled because it was surrounded by topographically protected sites and young forests of low fire risk. Other subalpine areas in Yellowstone National Park may be covered by predominantly late-successional forests

developing after a different series of major fires in the past, and here, recent fire suppression may have delayed the onset of the next major fire cycle. The magnitude of this delay, however, is probably well within the normal range of stochastic variation in fire intervals. Note that these conclusions apply only to subalpine ecosystems in Yellowstone National Park: at lower elevations where fires formerly recurred at shorter intervals and the period of effective fire suppression was longer, some significant ecological changes may have occurred (Houston 1973, Loope and Gruell 1973).

The current fire management plan probably will be effective in maintaining natural landscape patterns in the subalpine zone if most lightning-caused fires are allowed to burn naturally, including the very large fires. The results of this study indicate that managers should expect, and allow, an occasional fire covering many square kilometres; these are the fires that will exert a predominant influence on landscape composition and diversity for many decades to follow. Such large fires should not be viewed as unusual events occurring because of abnormally high fuel accumulations. Although fire suppression has modified natural fuel patterns in some other areas (Dodge 1972), I found neither evidence for unusual fuel accumulations in this area, nor any need for prescribed supplemental burning to reduce fuel loads.

An intriguing result of the landscape simulations for the last 200 yr was that some components of landscape diversity would have been higher at certain times under a selective or even a total fire control policy than with the natural fire regime (e.g., 1878: Figs. 10 and 11). The use of a carefully planned program of prescribed burning or timber harvesting would undoubtedly make it possible to maintain greater landscape diversity than occurs naturally. Although this might have some positive effects, negative effects would also be possible, and such an experiment would be wholly inappropriate in a natural area such as Yellowstone National Park (Houston 1971).

The long-term patterns in landscape composition and diversity shown in Figs. 8–11 underscore the recommendations of Wright (1974), Sullivan and Shaffer (1975), Pickett and Thompson (1978), and others that in the establishment and management of natural areas for conservation of biotic diversity, care must be taken (1) to set aside a large enough area to include a mosaic of all normal stages in community development, and (2) to allow natural processes of perturbation and recovery to occur unchecked. Otherwise, species and ecological processes restricted to particular successional stages may be lost. The very large-scale patterns of perturbation and recovery characteristic of the Yellowstone subalpine ecosystem probably necessitate a much larger natural area here than might be required in some other ecosystems where individual

perturbations are more frequent and affect a smaller area (Shugart and West 1981).

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Ecosystems of National Parks

National parks are unique in seeking to limit man
to nonconsumptive uses of the land.

Douglas B. Houston

The primary purpose of the National Park Service in administering natural areas is to maintain an area's ecosystem in as nearly pristine a condition as possible (1). This means that ecological processes, including plant succession and the natural regulation of animal numbers, should be permitted to pro-

ceed as they did under pristine conditions, and that modern man must be restricted to generally nonconsumptive uses of these areas.

These deceptively simple, and seemingly naive, ideas require explanation. Few of our parks are completely self-contained ecological units, and their

problems have been repeatedly cataloged (2-5). These areas have obviously been affected by modern man's overall disturbance of the biosphere, as well as by his more specific disturbances, including elimination and introduction of species, designation of artificial park boundaries, and suppression of natural biotic processes. I will not minimize these problems: an Everglades without water or with a jetport would be a travesty. I contend that, despite man's intrusions into the ecology of national parks, the pristine ecosystem relations in many of them are comparatively intact or have some reasonable potential for being restored. This sounds incongruous, since visitors to several of these areas number in the millions annually. However, it is necessary to recognize that the uses

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man makes of these parks are largely nondisruptive and nonconsumptive; that is, man does not supply or divert significant amounts of materials and energy to or from the park ecosystem, and he is not a significant part of the food chain. There are exceptions in almost every park to the concept of nonconsumptive land use, but I think it can be shown that the objectives for natural areas are realistic and that national parks illustrate a type of land use that makes it appropriate to recognize a unique park ecosystem.

Research and Management in the Park Ecosystem

The maintenance of a natural park ecosystem requires a unique approach to research and management. Unlike other forms of land management, management of a park ecosystem generally involves preventing or compensating for man's altering of natural ecological relations.

Effective management is aided by a research program that provides information which is interpreted in light of park objectives. Much of the research in parks is directed toward documenting pristine conditions and processes, determining the completeness of park ecosystems, and developing management procedures to maintain or restore the ecosystem. A complete ecosystem, as the term is used here, would have both cycling of materials and energy pathways comparable to those in pristine conditions. Lack of ecological completeness may take a variety of forms, for example, unnatural reduction or elimination of predator populations or a park's having only a portion of the historical range of a migratory species—a problem common to mountain parks with ungulate populations and parks with a diverse avifauna. Recognition of this problem is by no means new (2, 6); putting it into the context of the ecosystem and trying to evaluate and compensate for incompleteness is comparatively new (3-5, 7, 8). A goal of many research plans is to describe the park ecosystem in more quantitative terms. This is being done by concentrating research on key relations in a given park's ecosystem, with the hope that, through them, we may understand the whole.

Evaluation and restoration of natural factors that shaped the vegetation (the producer level of ecosystems) are under

way in many areas. Continued protection of the vegetation from the influences of man is all the "management" that is required in some areas. In others, the restoration of natural processes requires more active management. Natural fires have helped shape the vegetation of many areas, and their influence is being restored in the form of prescribed burns and by allowing naturally occurring fires to burn. The 7000-acre pinelands in Everglades National Park represent a fire-maintained forest of southern slash pine (*Pinus elliotii*). Prescribed burns have been carried out since 1958, and their effects have been documented (9). This program will be continued on a routine management basis. Fire also maintained the red fir (*Abies magnifica*) forests of Sequoia and Kings Canyon national parks (10). Prescribed burning was done on an experimental basis in these fir forests, and now naturally occurring fires above 8000 feet in the Middle Fork of the Kings River are being allowed to run their course. Fires also burned at 20- to 25-year intervals in the groves of sequoias (*Sequoia gigantea*) in these parks (11). Restoration of natural fires presents a problem in the sequoia groves. Past suppression has resulted in an accumulation of fuels and the development of an understory vegetation. Experimental prescribed burns and mechanical removal of accumulated fuels are being tried in these areas. The management goals are to reduce this unnatural fire hazard, restore a natural process, and provide a suitable habitat for sequoia reproduction (10). Plans to "restore" natural fires in the parks of the Rocky Mountains are in various stages of discussion.

The periodic attacks of certain of the native herbivorous insects upon susceptible trees in park ecosystems has no doubt occurred for millennia. Attempts at "control" are not compatible with the objectives of natural areas, and the deaths of susceptible trees by native insects should be recognized as a natural process. The mountain pine beetle (*Dendroctonus monticolae*) is responding to favorable environmental conditions in portions of Yellowstone National Park and is attacking stands of lodgepole pine (*Pinus contorta*). No attempts at control are being considered (12).

The maintenance of representative populations of native ungulates in natural areas requires an appraisal of ecosystem completeness. In the parks of

the Rocky Mountains, ecological incompleteness may result from having the historic winter ranges of wild ungulates outside park boundaries. Under these conditions, populations are managed by public hunting that is carried on outside the park boundaries (3, 7).

Ungulate populations that are year-long residents on ecologically complete ranges are of considerably more interest. An hypothesis being tested on some of these populations that occur in periodically severe environments is that they may not need artificial regulation; that is, the park ecosystem is complete enough to ensure that the numbers of these animals are regulated naturally. Four specific examples are given.

1) A study of the moose (*Alces alces*) population in Grand Teton National Park has shown that regulation of numbers occurs primarily through periodic winter mortality and by reduction in successful births after severe winters, complemented by the emigration of subadults (13). Regulation has also resulted from short-term fluctuations in the conditions of the willow (*Salix* spp.) forage sources on winter range areas. These fluctuations have not caused permanent deterioration of plants or adverse effects upon other faunal species.

2) An elk (*Cervus canadensis*) population of about 1000 animals lives year-long in the Madison, Firehole, and Gibbon river areas of Yellowstone Park (7, 14). Regulation appears to result from rigorous winters and limitations on food supplies, with the complementary actions of predators, parasites, and disease. The elk provide food for a population of grizzly bears (*Ursus arctos*), a remnant group of gray wolves (*Canis lupus*) (15), and a variety of smaller predators and scavengers.

3) The elk and mule deer (*Odocoileus hemionus*) populations in the Middle Fork of the Flathead River drainage in Glacier National Park appear to be naturally regulated (16). Rates of reproduction of both species have been low. Population stability over the past 20 years has resulted from low mortality, balanced against low recruitment. The availability of winter yarding sites in coniferous forests probably determines carrying capacity. Differences in winter yarding areas and forage preferences appeared to reduce interspecific competition and permitted coexistence of both species.

4) A population of 100 to 300 bison

(*Bison bison*) has annually wintered in the Pelican Valley of Yellowstone Park since establishment of the park in 1872 (17). This population has been subjected to reduction in numbers by man only twice after having been poached to near-extirmination about 1902. It is considered to be naturally regulated. Regulation has been accomplished by the effects of average and even mild winters on mortality and reproduction. This has resulted in long periods of near stability. Increases during particularly favorable periods have been offset by periodically more severe winters. Short-term occupancy of thermal areas during periods of extremely adverse conditions may permit survival of biologically essential components of the population.

Certain tentative conclusions may be drawn from these examples, since several of these populations appear to have characteristics in common (14). Realized annual recruitment to the population is low. Range conditions fluctuate, and some areas appear to be periodically "overgrazed," in terms of the usual criteria. Ungulates participate in plant successional processes and may be capable of reducing or eliminating remnant vegetation types that are no longer a number-limiting food source. Large predators represent only one of a complex of regulatory factors on ungulates and may have been overrated as a major control in harsh environments (18). However, it is still difficult to generalize upon the effects of predation (19). Once the existence of natural regulation has been determined from intensive research, the "management" of these ungulate populations will consist of monitoring population characteristics and habitat conditions.

This approach to the management of vegetation and native ungulates illustrates the uniqueness of park ecosystems. It follows that the criteria used in forestry or range and wildlife management, where vegetation and wildlife are harvested as a crop, do not necessarily apply to national parks. For example, having an elk population with a low rate of reproduction on ranges that appear temporarily overgrazed may be poor game management, but it is excellent management of a park ecosystem, as long as it is essentially natural. It is self-evident that the usual concept of "waste" (20) does not apply in parks; that is, the death of trees and ungulates is necessary to maintain ecological relationships.

Managing Man

Providing for the educational and esthetic enjoyment of man, while maintaining pristine ecological relationships, represents the greatest challenge in the management of natural areas. In broadest terms, man affects natural ecosystems by altering biogeochemical cycles and by quantitatively or qualitatively altering energy pathways. This latter influence includes such things as supplying energy to or diverting it from the system, altering the distribution and abundance of native species, and introducing exotic species.

Overnight camping, regarded as traditional and compatible with park objectives, is permitted under current policies (21). However, a natural ecosystem can absorb only a small number of these facilities, and the larger complexes (including lodges, housing areas, and so forth) have effects that extend beyond their immediate boundaries. For example, the disposal of sewage from such areas could alter energy pathways, as well as nitrate and phosphate cycles. The disposal of nearly 7000 tons of garbage annually within Yellowstone Park represents a substantial energy input and has contributed to management problems by altering the natural distribution of the grizzly bear (22).

Effects of the input of materials and energy into the ecosystem may be modified temporarily by refined treatments that prevent, or at least alter the form of, the input (23). This is being done in several areas. Management programs for the grizzly bear call for elimination of garbage as a food source, plus such related steps as increased campground sanitation and protection, and, perhaps, eventual removal of these complexes from prime bear habitat (22, 24).

To effectively resolve these conflicts with park ecosystems, major complexes should eventually be moved to at least the periphery of—and better still, outside—natural areas. The concept of maintaining large overnight facilities was developed in the early decades of this century, when modes of transportation were slower and population centers were further from parks (4). However, in this day of rapid transportation, there seems to be little real need for maintaining such facilities in the heart of a natural area.

Angling, as it is currently practiced in most natural areas, is a consumptive use of a natural ecosystem and may

cause substantial alteration of energy pathways. Angling is considered a traditional, albeit controversial, use of parks. Some people hold that angling represents an anachronism with present pressures and that it should be eliminated (4); others hold that fish populations should be fully exploited and supplemented by stocking waters with fish raised in a hatchery. Angling in some form will no doubt be continued in the foreseeable future. However, the practice of stocking waters with hatchery fish, solely to maintain angling, has no place within a natural area. Furthermore, I consider maximum sustained yields to anglers to be too disruptive of ecosystem relations. Various races of native cutthroat trout (*Salmo clarkii*) still occur in the parks of the Rocky Mountains, although their distribution outside the parks has been greatly reduced.

Management objectives within these natural areas are to maintain wild populations of these and other native fishes in the aquatic ecosystems and to provide "quality angling" (25). "Quality angling" stresses the recreational aspects of angling: fish may be caught and released, but comparatively few, if any, are intentionally killed. This approach to the management of wild fish is being tested in several areas.

Sightseeing, which is considered a nonconsumptive use of parks, may also alter energy pathways unless it is regulated. For example, visitors have so damaged certain accessible areas of the fragile alpine tundra of Rocky Mountain National Park that initial recovery from trampling may require decades; complete recovery, centuries (26). This alteration was aggravated by such consumptive acts as picking flowers and removing stones. Management actions that may help correct the situation include channeling visitor activities by developing well-routed and maintained trails, relocating parking areas, and developing a visitor education program to explain the nature of tundra ecosystems.

These examples of the influence of man on natural ecosystems illustrate something of the conflicts facing park managers. Despite these conflicts, it appears to be feasible to maintain natural relations—if it is recognized that park ecosystems have a finite capacity for absorbing certain of man's disruptive and consumptive influences. This capacity has been reached in many areas.

Interpretation of the Park Ecosystem

The explanation of natural phenomena to the park visitor is another function of the National Park Service. Interpretation includes exhibits at museums, visitor information centers, and along roadsides; hikes and evening programs conducted by Park Service personnel; and self-guiding trails and auto tours. In addition, most areas offer a variety of publications that explain features of the park.

Visitor interest in these facilities and activities appears to be high. Nearly 20 percent of the 2.4 million summer visitors to Grand Teton Park in 1969 used visitor centers and attended more formal programs (27). Over 50 percent of the visitors to Yellowstone National Park during 1970 visited at least one of the six visitor centers, and about 10 percent attended one or more evening programs or nature walks (28). During the past several years, interpreters have used the ecosystem concept as a vehicle for communicating an understanding of park philosophy. Museum exhibits and brochures describe in laymen's terms the park ecosystem and objectives in managing natural areas. A skilled interpreter can build an entire program around a park's ecosystem.

A quality environment does not yet rank high as a national priority, despite current public interest in ecological problems. The National Park Service has an opportunity to contribute to the promotion of an environmental ethic that extends beyond park ecosystems to those of outside areas, and to such problems as environmental degradation and rates of human population increase. This opportunity is being used, and hopefully more emphasis will be placed on environmental problems in future interpretive programs. The contrast between the ecosystem of an unpolluted river in a park and a river such as the Thames [where perhaps one-half of the energy input is from sewage and detritus (29)] might be enlightening to many visitors.

Summary

The preservation and maintenance of natural park ecosystems, with modern man's being restricted to generally

nonconsumptive uses of the park, represents one end of a spectrum of land use that extends through exploitation of natural ecosystems to the development of simplified agricultural ecosystems. Criteria for management of a park ecosystem must, of necessity, differ from criteria for other uses of land, since park management involves preventing or compensating for the influence of man. The objectives for natural areas appear to be ecologically feasible if it is recognized that these areas have a finite capacity for absorbing man's consumptive and disruptive influences. The interpretation of ecosystems to park visitors provides an opportunity to contribute to an environmental ethic that extends beyond the park environment.

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28. W. W. Dunmire, personal communication.
29. K. H. Mann, in *Advances in Ecological Research*, J. B. Cragg, Ed. (Academic Press, New York, 1969), vol. 6.
30. I thank G. F. Cole, C. J. Martinka, P. S. Hayden, and A. Murie for reviews of the manuscript. These and other research biologists of the National Park Service made unpublished data available for this article. Many of the ideas and arguments presented herein have not originated with me but have been formulated largely in discussions with these same gentlemen.

Effects of Natural Fires in Yellowstone National Park

In 1972, Yellowstone National Park began allowing some lightning-caused fires to burn themselves out. This program permits fire to play its natural role in the ecosystems of the park just as it did before the suppression activities of European man which began in the nineteenth century. All man-caused fires and those lightning-caused fires that threaten developments are still suppressed.

Once a fire burns several acres of forest it tends to persist until the winter snows come. Some have lasted for 10 to 12 weeks. During a stormy period no smoke may be visible for several days. Fires persist through these cold wet periods in rotten logs or in the duff of the forest floor protected by dense tree crowns. When fuels again dry out the fires often burn more forest.

The growth of the new biotic community begins immediately following the burn. Insects begin to utilize the new food source provided by freshly killed trees. Root stalks of many plant species begin to resprout. Preliminary results of research indicate eight species of birds may be eliminated from these forest areas but eight other species move into the newly created habitat. Some of these colonizing species are thought to be declining or are rare throughout their range, for example: Mountain bluebird and Blackbacked three-toed woodpecker. Large numbers of small rodents such as deer mice find adequate food supplies the first growing season even though plant cover is less than 10 percent.

By the third growing season the forest floor is approximately 70 percent covered by plants including fireweed, lupine, leafy aster, elk sedge, heart leaved arnica and about 20 other species mostly root sprouts of plants present on the forest floor before the fire. Seedlings of the next forest stage (lodgepole pine) become established. Plant growth is lush and vigorous because of abundant mineral nutrients available from the ashes and because of increased light levels. Elk, moose, and bears begin to forage in this abundant plant cover.

Fuels suitable for carrying another fire are quite rare for decades following the burn. Lightning strikes and even firebrands from a neighboring forest fire can only ignite small spots, which remain small because the fuels are discontinuous. With plant succession the probability that the area will burn again increases steadily. A mosaic of stands in different successional stages will provide both for species that require old mature forests and those that require the recently burned forest. This mosaic will also reduce the number of fire starts and limit fire size over time.

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Fire seasons summary, Yellowstone National Park, 1972-87

<u>YEAR</u>	<u>TOTAL FIRES</u>	<u>LIGHTNING CAUSED FIRES</u>	<u>PRESCRIBED NATURAL FIRES</u>	<u>PRESCRIBED NATURAL ACRES</u>	<u>TOTAL ACRES</u>
1972	21	15	4	1	4
1973	33	24	2	2	145
1974	38	28	7	830	1307
1975	26	18	9	2	6
1976	30	19	15	1551	1603
1977	29	18	8	10	67
1978	24	12	6	6	14
1979	55	30	20	10,520	11,234
1980	25	21	16	1	4
1981	64	57	28	20,240	20,595
1982	20	13	9	0	0
1983	7	4	4	0	0
1984	11	11	9	0	0
1985	53	43	42	33	33
1986	33	27	27	1	2
1987	35	29	29	960	964
TOTAL	= 503	369	233	34,157	35,978
AVERAGE	= 31	23	15	2,135	2,249

Compiled from park records by Roy Renkin, N.P.S. Research Division.

Natural Fires Out On Their Own	Natural Fires Initially Allowed To Burn, Then Suppression Or Containment Action	Natural Fires Allowed To Burn Into Existing Natural Fires - Too Close To Expend Resources On	Man-Caused Immediate Suppression	Natural Fires Immediate Suppression Action					
1. Rose 2. Crystal 3. Cougar 4. Maple 5. Lewis 6. Miller 7. Amethyst 8. Richards 9. Pelican 10. Cone 11. Passage	5/24 6/12 6/23 6/25 6/25 7/05 7/05 7/07 7/10 7/10 7/17	1. Shoshone 2. Fan 3. Red 4. Lava 5. Mist 6. Clover 7. Falls 8. Storm Creek* 9. Mink Creek* 10. Continental	6/23 6/25 7/01 7/05 7/09 7/11 7/12 7/29	1. Raven 2. Lovely 3. Factory 4. Shallow 5. Badger 6. Ridge 7. Fern 8. Sour	7/11 7/20 7/24 7/31 8/01 8/04 8/05 8/27	1. Observation 2. Grizzly 3. Narrows 4. Northfork* 5. Colannade 6. Norris 7. Hellroaring* 8. Huck*	6/09 7/12 7/14 7/22 7/28 8/16	1. Tower 2. Spring 3. Harebell 4. Hancock 5. Cub 6. S. Maple 7. Basin 8. Terrace 9. Forest 10. Peale 11. Boundary 12. Madison	7/15 7/17 7/23 7/28 7/30 7/30 7/31 7/31 8/04 8/11 8/12 8/13

*Fires origin outside of park

YELLOWSTONE FIRES

September 26, 1:00 p.m.

9

Here is a list of the fires and approximate perimeter acreages. To date, over 1.1 million acres in Yellowstone National Park (includes NF portions of Clover-Mist and North Fork Fires) and approximately 1.6 million acres in the Greater Yellowstone Area have been affected by fire. However, only about half of the vegetation has burned within many fire perimeters. Throughout the summer, 52 different fires have been started by lightning. Of those 52, eight are still burning inside the park. Fire fighters are working to control them. Any new fires will be suppressed as quickly as possible.

* * * * *

Clover-Mist Fire: 412,550 acres. Mist Fire started July 9. Clover started July 11. They joined on July 22. Shallow Fire started July 31. Fern Fire started August 5. These two fires joined Clover-Mist August 13. Lovely Fire started July 11 and burned into Clover-Mist on August 21. Estimated 83% contained. This fire crossed the Montana border near Kersey Lake. Growth was about 1,050 acres over the weekend. Acreage reduction is due to remapping. 1120 firefighters, 31 engines, 2 bulldozers, 9 helicopters.

Fan Fire: 23,325 acres. Started June 25. No change. The fire was contained on 9/2. One crew is completing mop-up.

Hellroaring Fire: 83,888 acres. Started August 15. This fire is 100% contained. Mop-up and rehabilitation work continues.

Huck/Mink Complex: 225,500 acres (includes Mink Creek Fire acreage in Bridger-Teton NF). Started August 20. Caused the evacuation of Flagg Ranch. The fire was 100% contained on 9/15. No estimated date of control. Mop-up and rehabilitation work continues.

North Fork: 400,100 acres. Started July 22 by human. Split from Wolf Lake Fire at Gibbon Falls. This fire is about 50% contained with 100% containment expected by mid-October. Some increase in fire activity is expected due to dry, windy weather. 1339 firefighters, 8 bulldozers, and 4 helicopters.

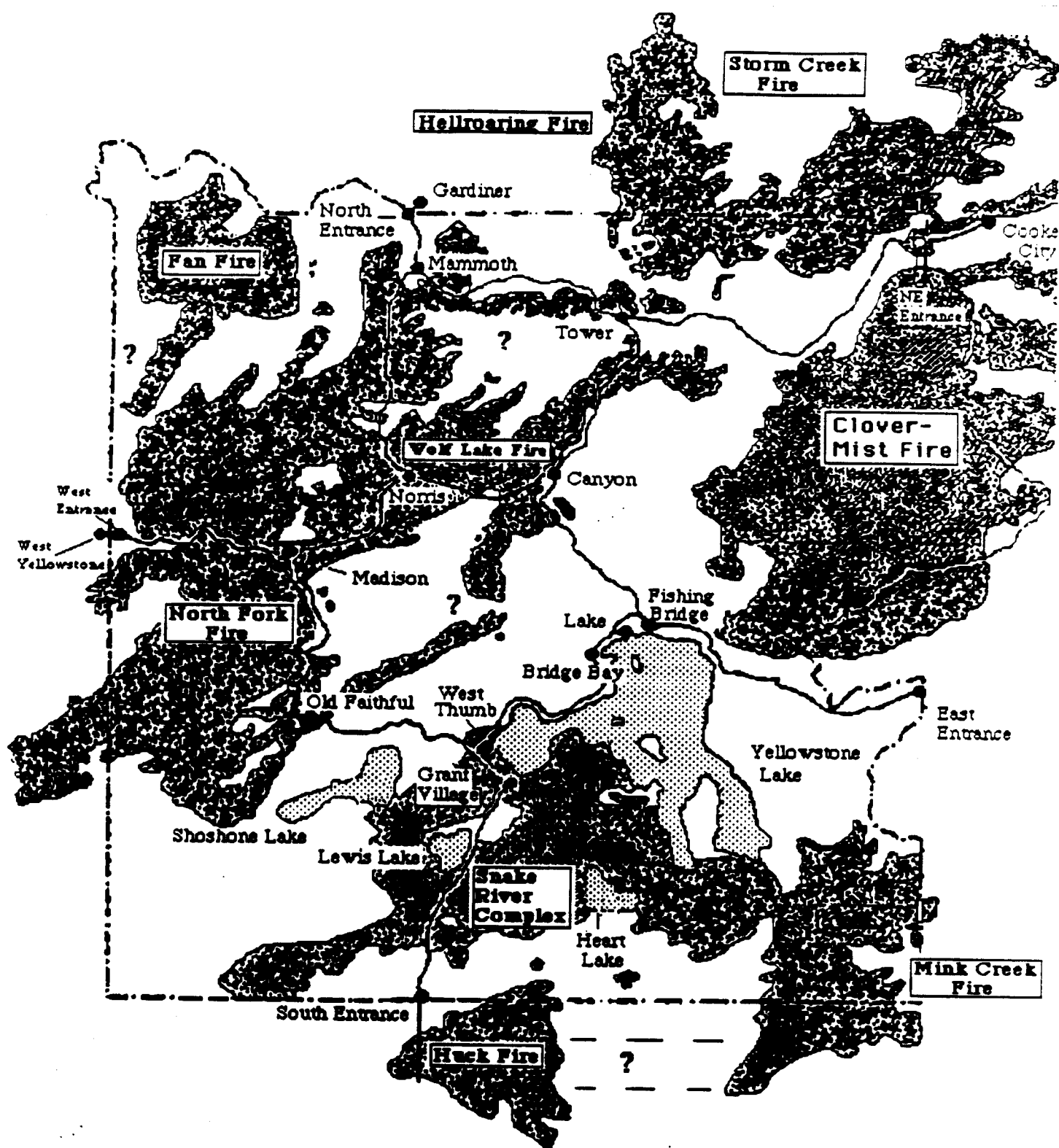
Snake River Complex: 224,000 acres. Red Fire started July 1. Shoshone Fire started June 23. Joined August 10. Falls Fire started July 12. Red-Shoshone Fire joined the Mink Fire on August 31. Acreage includes Continental-Ridge and Mink Creek fires. The fire was declared 100% contained on 9/19 at 1700 hours. Mop-up operations and rehabilitation work continues. Fuel modification in Lake area continues as well. 459 firefighters, 1 engines, 1 helicopters.

Storm Creek Fire: 107,847 acres. Started July 3. This fire was declared 100% contained on 9/17. Mop-up operations continue in the Soda Butte and Pebble Ck. areas.

Wolf Lake Fire (includes Mammoth Complex): 107,460 acres. Fire grew only 20 acres over the weekend despite dry weather and high winds. Most military crews are leaving by 9/28, and they will not be replaced. Estimated date of containment still depends on receiving additional precipitation. 1099 firefighters, 12 engines, 9 helicopters.

Crews on many of the fires continue to demobilize. Unified Area Command operations in West Yellowstone have been shut down. As a result, accurate information on crew sizes and resources for some of the fires was not readily available.





YELLOWSTONE FIRES

September 26, 1988, 1:00 p.m.

Since mid July more than 2,000 (and currently, over 4,000) fire fighters have been actively working to contain or suppress the different fires burning in the Yellowstone area. This year the park has experienced a drought along with high daytime temperatures, low humidity, and strong, gusty winds. These conditions caused fires to grow and burn actively. They also have made it difficult to contain or suppress the fires.

INFORMATION PAPER No. 16
Yellowstone National Park
March 1972

Don G. Despain
Research Biologist

FIRE AS AN ECOLOGICAL FORCE IN YELLOWSTONE ECOSYSTEMS

Fire is a natural force that has been operating in the Yellowstone ecosystems since they originated. Since 1931, records show 22 fires per year on the average have been started by lightning. Fire scars on old Douglas-fir trees indicate an average frequency of one fire every 30-60 years in the Lamar River valley. Other indications of old fires are even-aged stands of lodgepole pine throughout the park, and charcoal which occurs commonly in the soils of Yellowstone. We can assume that the ecosystems of the park are in some way adapted to this environmental force, perhaps even dependent on it.

Many plants growing on the forest floor are adapted to survive at a subsistence level and dependent on vegetative means of reproduction. They cannot exist forever under a forest canopy and are dependent on periodic release. When the overstory is destroyed by fire these plants are released to produce much more luxuriant growth. Food reserves are replenished, allowing the plants to live through the next period of canopy closure. During these periods sexual reproduction also becomes possible, allowing the plants to maintain genetic diversity.

Douglas-fir trees are adapted to fire by having thick bark that resists damage by ground fires. In the past there were probably a number of open savanna like Douglas-fir stands kept open by periodic ground fires that were frequent enough to keep most young Douglas-fir trees from becoming part of the overstory. The widely scattered large fire-scarred trees in some of the dense Douglas-fir stands in the valleys of the Lamar and Gardiner rivers are probably remnants of these communities.

Lodgepole pine trees produce two types of cones: one that opens at maturity and a serotinous type that opens after it has been heated by a fire. The serotinous cones insure a ready seed source for seedling establishment immediately after a fire. Seeds from species without serotinous cones--such as Engelmann spruce, subalpine fir, or Douglas-fir--must be carried into the area from surrounding seed trees by wind, squirrels, or other agents.

Many lodgepole pine forests have shade tolerant spruce and fir saplings growing under the pines. If fire is excluded long enough, these lodgepole pine forests will be replaced by spruce-fir forests. Even a climax lodgepole pine forest will change in character when fire is excluded. As trees that established immediately after the fire reach maturity and are thinned by disease or other natural agents, an understory of young lodgepoles begin to develop, and the stand becomes quite diverse in age. The large expanses of even-aged lodgepole pine forests are a good example of communities dependent on fire for their existence.

The spread of tree disease and the extent of individual forest fires are likely to be reduced when a natural fire regime prevails. Young stands are less susceptible to disease, and fuel levels in them are lower. The probability of a disease or fire spreading over large areas is reduced when the area is broken into mosaics of different age groups.

Many plants require at least a moderate amount of sunlight and cannot compete successfully with plants that establish in heavily shaded sites. Some plant communities are dependent on the removal of the climax forest overstory to allow for their establishment. These are called pioneer communities because they are the first to inhabit newly released sites. It is evident that the incidence of fire determines the place of these and other pioneer communities in a landscape.

Fire has also acted in the past to prevent the invasion of trees into grassland areas. Micro-habitats suitable for tree seedling establishment are rare in a grassland community, but when a seed reaches these micro-habitats during a favorable year, a tree may become established. The coming together of viable seed with a suitable micro-habitat is a rare but constant event near a forest edge. Once the tree is established and grows it begins to influence the environment in its immediate vicinity. More tree habitat is created and a small island of forest is created. These islands then coalesce, more grassland is converted to forest, and the process starts over. Periodic fires kill the small trees before they have a chance to become islands maintaining an equilibrium between forest and grassland.

Mineral nutrients are very important to plants, often acting as limiting factors. With the possible exception of nitrogen, the amount of nutrient available to a plant community is governed by what is available in the soil. The mineral nutrients of an ecosystem tend more to cycle within than to flow through the system. They go from the soil to the wood and leaves of the plants to the litter and back to the soil. Rainwater and weathering of minerals bring mineral elements into the system; water and animals remove them. Fire has a strong influence on the rates of some of these processes. Minerals tied up in litter and wood are released either slowly by micro-organisms or very rapidly by fire. Heat from fire may also be instrumental in hastening the weathering of soil minerals, allowing release of more mineral elements. Following a fire this abundant supply of soluble minerals is rapidly taken up by increased plant growth. A large part is also removed from the system by runoff water or leaching. Grassland species require more mineral nutrients than pine forest species. Thus loss of nutrients from forest communities may be a necessary mechanism for the maintenance of the forest ecosystem.

NATURE AND MAN IN YELLOWSTONE NATIONAL PARK

Yellowstone National Park is administered as a natural area. Such areas are to preserve natural environments and native biota as an integrated whole (i.e. ecosystem) and to provide for the public enjoyment of same in ways that maintain natural conditions. Natural conditions exist to the extent that man does not change things from what they would otherwise be. Obviously changes will occur from natural processes and these need to be distinguished from those due to man. Management in natural areas is restricted to protecting against, removing, or compensating for the activities of man that cause departures from natural conditions.

The retreat of glaciers about 30,000 years ago permitted vegetation and wild animals to occupy the region that became Yellowstone Park. Primitive man arrived about 10,000 years before present and subsisted in small numbers until about 100 years ago when the park was established. All other native species are still present. With the possible exception of the Rocky Mountain wolf, representative populations of all native wild animals are yearlong residents. Additional numbers of elk and mule deer use the park in summer and make annual migrations from and back to wintering areas in Wyoming, Montana, and Idaho.

The present effects of modern man on the park environment and its resident biota are diagrammed on Fig. 1. As shown, less than 1% of the park's 2.2 million acres is permanently altered as roads or facilities that presently accommodate over 2 million visitors each year. The disposal of effluents and wastes from existing facilities does not appear to be causing departures from natural conditions in the remainder of the park.

The remainder of the park represents an ecological system where natural conditions are to be maintained or restored. As indicated on Fig. 1, the extent to which man suppresses naturally-caused fires is causing this system to be different from what it would otherwise be. Departures from natural conditions are greatest in the park's grassland areas which burned on the average every 20-25 years, and least in forest habitats that burned every 100-200 years.

Other measurable departures from natural conditions occur from man's past and present exploitation of native fishes. Less easily corrected departures occur in some portions of the park from past introductions of exotic fishes and plants. Minor departures also persist from eras when native predators and herbivores were artificially controlled, but these are being erased with the passage of time.

Overall, Yellowstone National Park appears to be sufficiently large and ecologically intact to make the objective of preserving a natural ecosystem of mountain environments and native biota obtainable. The objective of providing for the public enjoyment of same in ways that maintain natural

conditions also seems feasible, but only with limits on the numbers of visitors and the kinds of activities that can be accommodated. Most present departures from natural conditions can be corrected by not interfering with natural processes, by the appropriate regulation of humans, or the passage of time. Obviously, the preservation of natural ecological systems requires a "let it be" philosophy. Human judgments of what is good or bad in such systems can only be appropriate within the context of what is or is not natural.

Man's effects on wild animals that are not yearlong residents of the park present some conflicts with the attempts to restore and maintain a natural ecosystem inside the park. A viable population of wolves may only be restored if this species is also adequately protected on certain adjoining state lands. Mountain lions and grizzly bears will also need to be protected on some adjacent lands to occur in natural densities within the border regions of the park. The hunting of elk and mule deer on adjacent lands does not cause serious conflicts, unless such activities restrict migrations from the park.

Recommended Reading

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- Houston, D. B. 1971. Ecosystems of national parks. Science. 172: 648-651.
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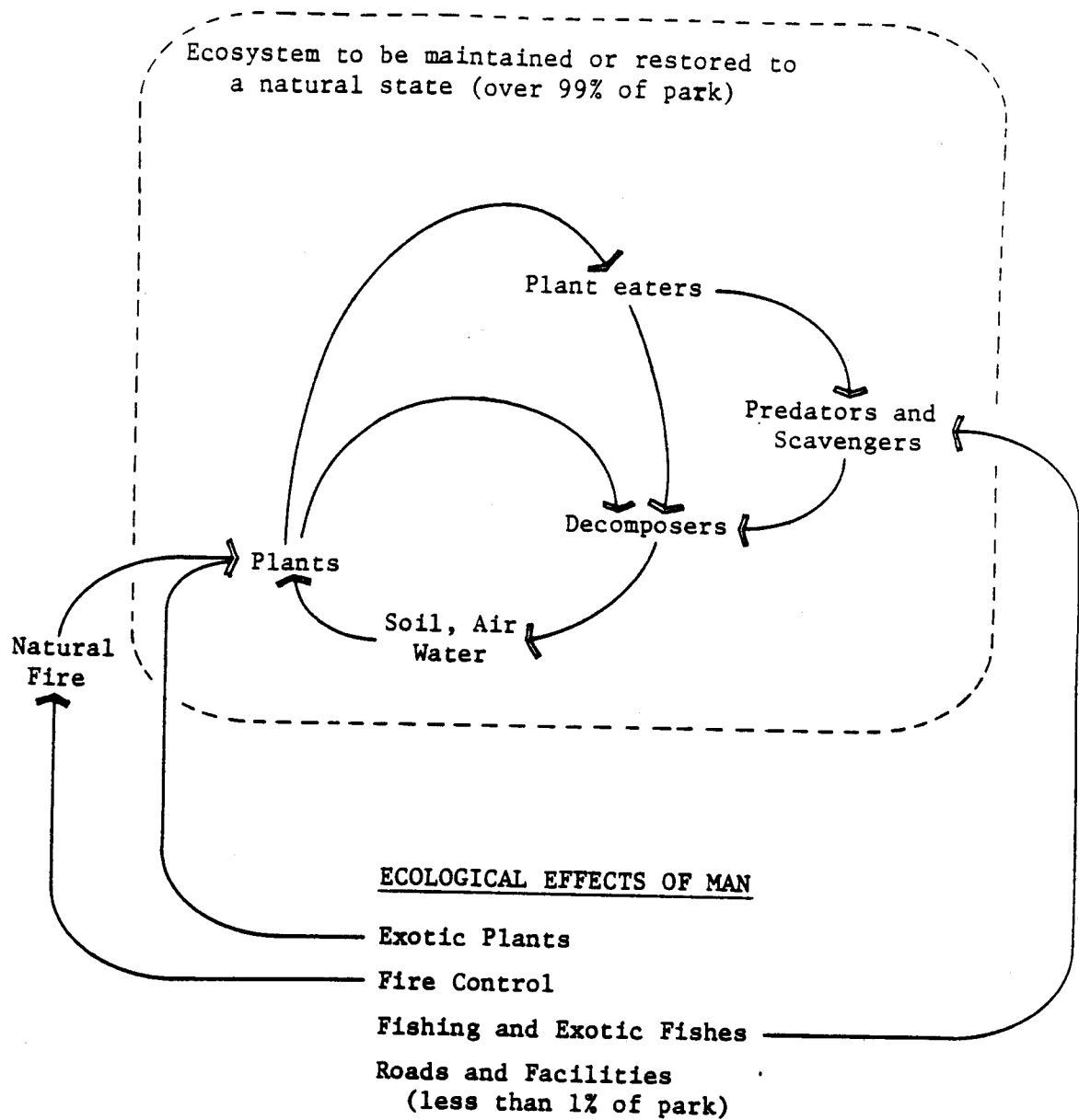


Figure 1. Present ecological effects of man on the cycling of nutrients in the park ecosystem.



THE

BUFFALO CHIP

YELLOWSTONE NATIONAL PARK
Hot August of 1988

FIRE EFFECTS ON YELLOWSTONE'S NATURAL RESOURCES

(The following are summary statements to help park staff answer questions on the general effects of fire on the ecosystem. These have been prepared using some published literature on past fires in other areas, and from observations thus far during the park's 1988 fire season. Keep in mind that effects will vary from area to area, and we will be learning a great deal from studying Yellowstone's natural recovery from fires in the coming decades. In a later issue, perhaps we will all have more time to report what we have learned thus far from the Fires of 1988.)

WILDLIFE by Sue Consolo and Mary Meagher

General summary: Species survival should be stressed, as opposed to individual animals. Literature reports (from 22 studies) in birds, the greatest loss in foragers of the tree trunk and canopy, and greatest gain in ground feeders; in mammals, the loss is in forest species and the gain in grass and shrub forms. Grizzly bears, elk, bison, deer thus should generally benefit from improved grass and shrub forage in the next 1-5 years. Smoke is of little consequence to wildlife; increased heat, light, and change in vegetative structure is more important. Fire may have a "cleaning effect", removing internal and external parasites.

MAMMALS

Short term: Effects vary based on their mobility, ability to find refuge, and size of fire. Small mammals (rodents, squirrels, mice, etc.) are most likely to flee, but may find refuge in burrows if they have adequate ventilation. Cause of death, when it occurs, is more likely from suffocation than from burning. Large mammals may flee from fires, or may show no major reaction.

Radio-collared elk have been monitored within burn perimeters for the entire summer in the Red-Shoshone and Clover-Mist Fires. Movements appear to be small, as they move between unburned spots. Many aerial observers have mentioned seeing bison, elk, and bears surrounded by burnt or burning spots. Radio-collared mountain lions also show no apparent change in movements as a result of fires. Moose, elk, and bison appear to be inhabiting their normal areas. Research shows some wildlife are attracted to fires, presumably looking for prey driven from their homes. Carnivores, such as coyotes,



foxes, and bears, will take advantage of small mammal availability. Dr. Linda Wallace has observed bison to face flames and travel into oncoming prairie fires in Oklahoma, though that has never been recorded in Yellowstone.

Long-term: Habitat modification is the major effect (as opposed to direct mortality); it varies greatly for different species. Generally, large animals (deer, elk, black bear, moose, beaver, cougar, coyote, grouse all reported in literature) increase in number after fires as a result of changes in plant succession and increase in nutritive forage. Fire may temporarily displace species dependent on late stages of plant community development (pine marten, wolverine.)

BIRDS

Short-term: Literature again reports birds generally show no fear of fire and some are attracted to a smoking landscape (insectivores and birds of prey especially.) McEneaney reports some direct mortality of unfledged birds in Red-Shoshone Fires. He observed an adult pair of osprey tried vainly to continue feeding fish to their offspring, which perished in the fire. Rangers report increased raptor activity (probably hunting small mammals who have less ground cover to protect them now) on the Clover-Mist and North Fork Fires.

Long-term: Increased sunlight to the forest floor, vigorous vegetation growth may increase species diversity in the first years after fire. Ruffed, sharp-tailed, and blue grouse, and some waterfowl are reported to be favored by burns. Most breeding species of birds stayed after fire in studied areas, only a few species moved out, and a few new species moved in. Raptors and cavity nesters (woodpeckers, mountain bluebirds) likely benefit from the increase in nest trees.

PROSPECTS FOR LARGE UNGULATES THIS FALL AND WINTER by Mary Meagher

Large ungulates, such as bison and elk, will be influenced considerably this year by drought. Water flow and weather records indicate the summer of 1988 to be far more extreme than the summers of the 1930's drouth. Also, these ungulate populations are at higher numerical levels because of the series of recent mild winters. They have already filled up their habitat - a normal process - and are showing movements characteristic of what we call upper equilibrium densities. These are never static under natural conditions, but are expected to show fluctuations according to changes in the environment. The 1988 fire season is likely one of those times.

The park's large ungulates are little bothered or displaced by fire, but the fires of 1988 are also a product of the drought. Thus, drought has set the



stage for several events, including a probable lowering of ungulate numbers. If another below average winter comes, we will likely see larger bison movements on the northern winter range compared to last year, and more elk will migrate outside park boundaries. If winter is average to above-average in snowfall, those effects will increase further, and we would expect more winterkill. In the park interior we also expect some winterkill, as usual.

Even without fire, these events would occur. Populations of ungulates (and other wildlife) have inhabited this area since the Pleistocene ice melted some 10,000 years ago, and have gone through many cycles of weather involving drouth, fire, and extremely severe winters.

BEARS

Short-term: Grizzly bear production looks to be good this year. The key factor that biologists monitor is sows with cubs of the year. Data this year indicates 14-16 grizzly sows with cubs of the year in the ecosystem. (This compares with a record 24 sows with cubs of the year in 1986 and 13 in 1987. The goal is a running three-year average of 15.)

The drought can be expected to have far more influence on bears' movements and foraging activities than will fire. Typically in mid-August bears (both black and grizzly) shift to food sources other than those used in early summer, as plants and their stage of growth change seasonally. 1988 does not appear to have produced a good whitebark pine crop, which has been recognized as a key fall food for grizzlies. In the absence of this highly preferred food, and to supplement it in any year, bears seek other foods such as still-succulent vegetation, roots, and berries. Due to drought, bears may wander more widely this fall in their efforts to find vegetative substitutes for whitebark pine nuts. This may cause a higher than usual potential for bear-human conflicts, or result in bears being seen in unusual locations.

However, bears can benefit in the short-term from fires. They, like coyotes and raptors, may have increased access to rodents, which are more easily seen after fire removes ground cover used by small mammals. Data shows bears have increased their intake of insects in recent weeks. Satellite locations on a radio-collared grizzly in Yellowstone show his movements remain in and around the burn perimeter of the Clover-Mist Fire, which is also the area he foraged last year. Bears have been sighted within burn perimeters, though no grizzly-human conflicts have yet occurred with fire crews. If this winter results in a more significant winterkill than recent mild winters, bears will benefit from an increase in carrion next spring when they emerge from denning.

Long-term: Fire releases nutrients locked up in extensive, older-aged forest stands, old sagebrush, and grass litter. Bears, especially grizzlies, should

benefit from the increased production and nutritive content of vegetation and meadow areas in the first decade after the fires. In mixed forest stands (i.e., whitebark pine, spruce and fire together), whitebark may be favored by fire and grow well in opened areas. This could result in an eventual increase in another of the grizzly's preferred foods. Generally, fire tends to produce a mosaic of vegetation patterns, which benefits a wide variety of interrelated wildlife species.

FISH AND FISHERIES by Ron Jones

The fires in Yellowstone will have some good and bad effects on the fisheries, however the **detrimental** effects should be **short-lived** and the **positive** effects will be **long-lasting**. The detrimental effects will come from increased siltation in streams which can affect fish reproduction and stream productivity. The severity of the siltation problem will be governed by precipitation patterns following the fires. Normal fall precipitation will cause minimal siltation; however, abnormal precipitation patterns, such as several inches of rain in a short period of time, could cause substantial siltation problems. These will probably be more serious in the Lamar River and Soda Butte Creek drainages, which normally produce the most sediment due to highly erodible soils and steep terrain. Greatest siltation loads will be carried by the 1989 runoff period. Runoff normally carried 98% of the yearly sediment load.

Positive effects of fire come from nutrient transport of forest ashes into the aquatic systems, and increasing organic material from riparian and instream vegetation which occurs after removal of the forest canopy. These changes plus increased water temperatures translate into increased aquatic productivity, which enhances the fisheries.

The extended drought will have a greater detrimental effect on the fisheries than will the fires. Streamflows are at an all-time low and the smaller streams are already being impacted by low flows. The larger streams will be severely affected if the drought continues into 1989. Low flows restrict the streams ability to over-winter fish and food production and living space are greatly reduced.

FIRE EFFECTS ON SOILS IN YELLOWSTONE PARK RESULTS OF PRELIMINARY SAMPLING

Yellowstone Park is now in the middle of the driest summer in recorded history. Lightning caused wildfires have burned over 450,000 acres so far this year. Yellowstone Park policy permits undisturbed burning in appropriate areas. Effects of fires are still studied however, to gain information on natural processes, to identify potential extra-Park effects, and to rehabilitate areas disturbed by fire suppression activities. Following is a summary of potential effects of fire on soils, and some results of initial sampling in two areas of Yellowstone Park.

GENERAL EFFECTS OF FIRE ON SOIL

Soil heating is dependent on fire conditions (duration, intensity, temperature, etc.), soil properties (texture, organic matter content, rocks, etc.), and site conditions (slope, litter layer, soil moisture, soil temperature, etc.). With given fire conditions, however, the degree of soil heating is primarily dependent on soil moisture status, organic matter (litter layers and in the soil itself), and soil texture.

The processes of heat transfer into soil are complex, but soil water is probably the most influential factor in its movement. Vapor flux is the most important process until the soil is dry. Water has a high conductivity, but also has a high heat absorbing capacity. As heat enters the soil, water will absorb that heat, and the soil temperature will not rise above about 212 deg. F. until all water has been evaporated or moved into lower layers. Then, conduction and convection become more important. A 20% to 70% reduction in heat conduction in moist versus dry soils has been measured.

Soil texture influences heat transfer. Quartz sands have about three times the heat transfer rate of clay minerals, so clayey soils transfer heat much more slowly than sandy soils. Litter layer thickness, composition, and moisture status also influences soil heating. Thick, moist layers of well decomposed litter can reduce soil heating by a large factor. However, these layers can burn and markedly increase the duration of heating, and can keep heat at the soil surface, allowing increased penetration to lower layers.

There is conclusive evidence that periodic burning (of moderate to light intensities) has little adverse effect on physical and chemical properties of soils. The exception is fine textured soils on steep terrain, where there may be increased erosion due to infiltration reduction and runoff increase.

GENERAL CLASSIFICATION OF SOIL EFFECTS

LIGHT INTENSITY: duff, debris partly burned, soil normal color: probably about 390 deg. F (200 C) on the soil surface; root crowns and surface roots will resprout; potential surface erosion has not significantly changed.

MODERATE INTENSITY: duff consumed, some woody debris left; soil brown to reddish brown; 390-930 deg. F. (200-500 C) on the soil surface; potential surface erosion may increase somewhat; soil are only slightly water repellent, and not uniformly so.

HIGH (OR SEVERE) INTENSITY: wood/duff totally consumed, soil orange-reddish with localized conglomerations; 1200 deg. F. (650 C); crusting of soil surface can significantly increase soil erosion potential; water repellency is widespread and severe.

RESULTS OF SAMPLING ON THE RED AND SHOSHONE FIRES (JULY, 1988)

Six sites on the Red and Shoshone Fires were evaluated for soil effects. Samples were taken from four of these for display and for organic matter analysis. Sites on the Red Fire illustrate moderate to light soil heating intensity. Litter (duff) was almost completely consumed. Soils were of normal color 2-5 cm beneath the surface. Plant roots and rhizomes were apparently alive at these shallow depths. The Shoshone Fire was similar, with the exception of high intensity under downed logs. Temperatures at about 5 cm were still above 380 deg. F. a day after the flaming front had past. These severe effects are infrequent in this area. Both sample areas had about 50% unburned area. Burned areas were black with all surface vegetation destroyed, and all trees killed. The above illustrates that even with apparently high heating, the soil is generally still a viable reservoir of life for the next growing cycle.

The above results apply only to these fires. Further sampling will be completed on the Fan, NorthFork and Clover-Mist fires, because these are burning in different landform/soil types. The soils office has a tray of burned and unburned soils. Stop by and we will show them to you.

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AIR QUALITY FACT SHEET

Because of health concerns about poor air quality due to forest fire smoke, several monitors have been installed in the park and adjacent communities. Currently, there are air quality monitors at the Northeast Entrance, the Mammoth fire cache, and the Gardiner Ranger Station. We are in the process of setting one up at the West Entrance also, and there has been an on-going air quality monitoring station running at Lake Ranger Station for 1 1/2 years. The station at Lake was mandated as part of long-term monitoring of all "Class I" airsheds, which includes many national parks and wilderness areas. It provides baseline data on the most pristine airsheds in the country. Alice Siebecker and several seasonal rangers at Lake have been instrumental in running this station, in cooperation with the WASO Air Quality Division. The other stations are temporary, installed this month to monitor particulate matter related to fires.

At Cooke City, Gardiner, and West Yellowstone, equipment measures "TSP", or total suspended particulate. It gives a numerical reading of the dust, dirt, and particles in the air. At Mammoth, in addition to TSP, equipment has been installed to measure PM-10, which is a more accurate assessment of the portion of TSP attributable to smoke, and a consultant will do some short-term monitoring of SO also. Both TSP and PM-10 monitors measure suspended particulates over a set time period. Equipment filters are currently changed every 12 hours and sent to Helena for analysis. The State of Montana's Air Quality Division then telephones the results of the analysis to the Resource Management Office.

The National Ambient Air Quality Standard for suspended particulates is 150, based on a PM-10 instrument. TSP monitor readings can be converted to PM-10 readings by multiplying by a factor of .8. A score of 150 is the national average of particulates for a 24-hour period, and the standard. Above that, pollutants may pose a possibly significant health risks to infants, the elderly, and persons with respiratory difficulties or cardiovascular impairments. A numerical reading of 350 initiates a First Stage of Pollution Alert; 420 is a Warning of Pollution Alert, in which the public is notified to take precautions, and 500 initiates a Pollution Alert. Under full alert, factories, and wood burning activities would be restricted to reduce the threat to the public health.

Results thus far from the Gardiner readings:

<u>DATE</u>	<u>PM-10 LEVEL</u>
8-12-88	118
8-13-88	50
8-14-88	65
8-15-88	94
8-16-88	119

8-17-88	No Reading Obtained
8-18-88	125
8-19-88	129
8-20-88	No Reading Obtained
8-21-88	No Reading Obtained
8-22-88	262
8-23-88	210
8-24-88	178

8-25-88	Day*	281
	Night	203
8-26-88		169
8-27-88	Day	53
	Night	89
8-28-88	Day	111
	Night	105
8-29-88	Day	259
	Night	227

* Because of the high readings obtained on August 22-24, 12-hour rather than 24-hour readings were initiated.

When readings exceed 150, the State of Montana Air Quality Bureau recommends that people 1) reduce or eliminate outdoor exercise or strenuous activity, and 2) reduce exposure to highly visible particulate levels by staying indoors and eliminating outdoor ventilation. Those people experiencing respiratory or other problems from smoke, especially persons with chronic breathing or other health problems, should use extra caution to limit exposure. This includes leaving the area if necessary. Persons with continued difficulties should seek medical assistance.

The Resource Management Office has set up this program with the cooperation of many persons. Fire accounts are paying for the monitoring, and staff from the Northeast Entrance, West Entrance, North District, and the Gardiner Forest Service office are collecting data. The WASO Air Quality Division and the State of Montana Air Quality Bureau have provided equipment, data analysis, and expertise.

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