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# FIRE AND LANDSCAPE DIVERSITY IN SUBALPINE FORESTS OF YELLOWSTONE NATIONAL PARK[1]

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*Abstract.* Fire history was determined by fire scar analysis in a 73-km$^2$ 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-km$^2$ 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-km$^2$ 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 interspersion 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 interspersion 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 objective 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 $km^2$, 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-$km^2$ 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 1972*a, 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 $\approx$100 cm annually in the eastern and northern portions of the watershed to $\approx$150 cm in the southern and western parts. Most of the

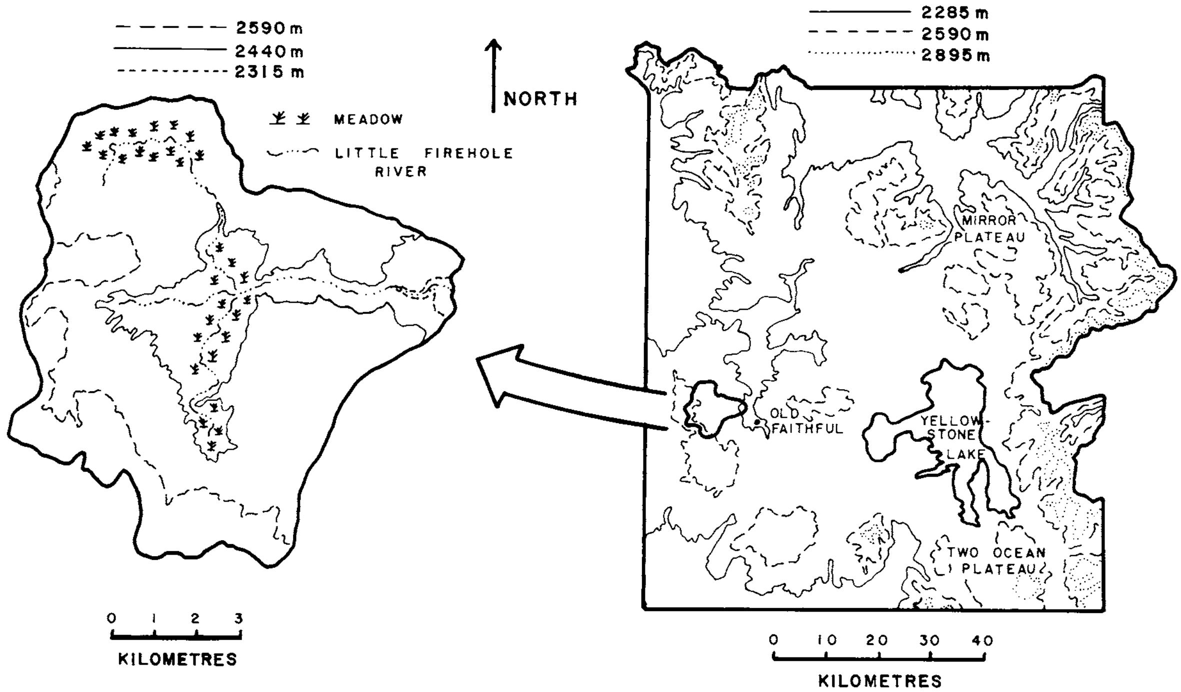


FIG. 1. Map of Yellowstone National Park, showing the location of the study area, and a map of the Little Firehole River watershed, showing major topographic features.

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 $km^2$ 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 $km^2$ 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.

| | Age in years | | | | | | |
|---|---|---|---|---|---|---|---|
| | Pico/Cage habitat type* | | | | Abla/Vasc habitat type† | | |
| Community 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 Abla/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 $\leq 1$ 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 $\approx 7$ km$^2$, 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 $\approx 4$ km$^2$, appear relatively stable in composition and structure, with no obvious secondary successional trends. Finally, small rock outcrops, boulder fields, and steep, rocky slopes cover $\approx 1$ km$^2$ 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 Sneck (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 ($\pm 20$ 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 McMinn 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 $\pm 2$ yr, between 100 and 200 yr ago: $\pm 3$ yr, and over 200 yr ago: $\pm 5$ 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 $\approx 1900$, 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 $\approx 20$ 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/$\bar{x}$) × 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 decrease 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 Abla/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 ($\leq$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 1980*a*, *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 dicontinuities 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.

| Index | Definitions |
|---|---|
| 1. Relative richness ($R$) $$R = \frac{T}{10} \times 100$$ | where $T$ = number of different community types present. (Maximum possible number is 10.) |
| 2. Relative evenness ($E$) $$E = \frac{H2(j)}{H2(\max)} \times 100$$ where $$H2 = -\ln \sum_{i=1}^{T} p_i^2$$ | where $H2(j)$ = modified Simpson's index (Pielou 1975) computed for landscape $j$<br>$H2(\max)$ = maximum possible value of $H2$ for $T$ community types<br>$P_i$ = proportion of total landscape area covered by $i^{th}$ community type<br>$T$ = number of different community types present |
| 3. Relative patchiness ($P$) $$P = \frac{\sum_{i=1}^{N} D_i}{N} \times 100$$ | where $N$ = number of boundaries between adjacent 5-ha cells in the watershed<br>$D_i$ = dissimilarity value for the $i^{th}$ 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-km$^2$ 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 Abla/Vasc) 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 ($H'$;

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 Abla/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 Abla/Vasc forest | | | | | | | 0 | .3 | .2 | 1.0 |
| Riparian forest | | | | | | | | 0 | .8 | 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 Abla/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),

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

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 Abla/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, Abla/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.

| | | All fires | | Major fires | | Fire frequency (fires·100 km$^{-2}$·yr$^{-1}$) | |
|---|---|---|---|---|---|---|---|
| | Area (km²) | 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 |

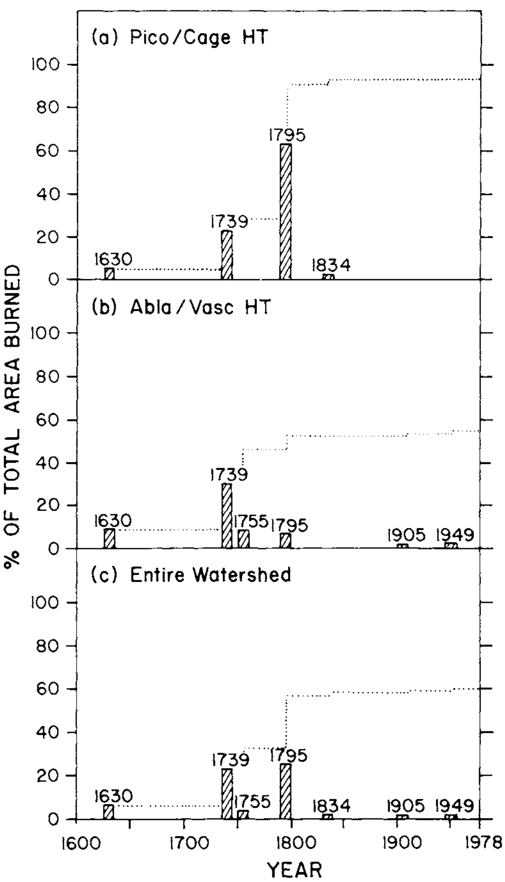


FIG. 2. Sizes of documented major fires since 1600 in the Pico/Cage habitat type (HT), Abla/Vasc HT, and entire Little Firehole River watershed, expressed as percent of total area in the habitat type or the watershed. The dotted line shows the cumulative area burned since 1600.

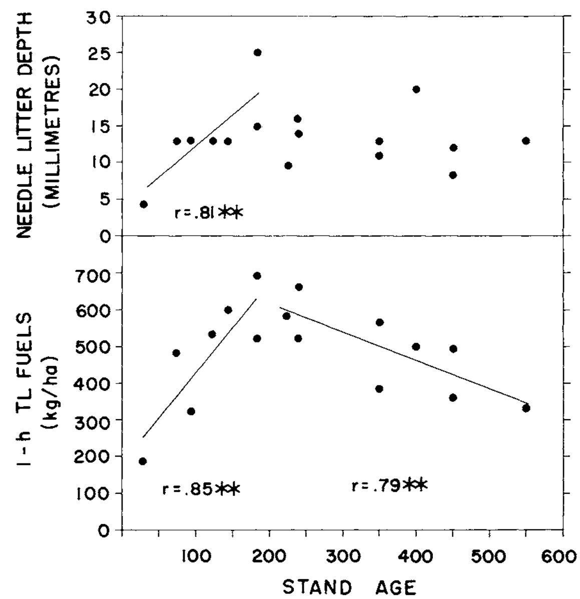


FIG. 3. Changes in small fuels capable of supporting ignition and initial fire spread along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero (** $P < .05$).

### *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. Bevins 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 watershed, 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 fireline, 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).

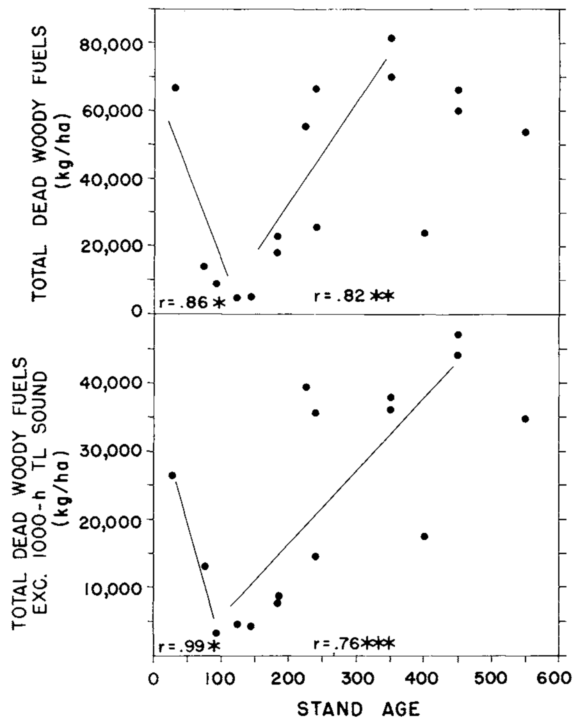


FIG. 4. Changes in total dead woody fuels and in total fuels excluding 1000-h TL sound fuels along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero (* $P < .1$, ** $P < .05$, *** $P < .01$).

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-*

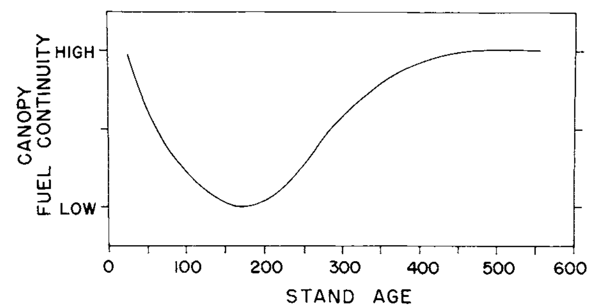


FIG. 5. Qualitative changes in total canopy fuel continuity (a composite of vertical and horizontal continuity) along a chronosequence of upland forest stands.

*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

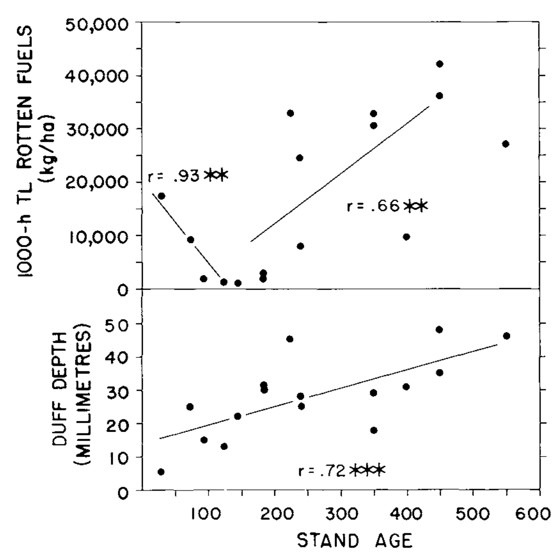


FIG. 6. Changes in fuels in which a fire may persist during periods of unfavorable weather along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly nonzero (** $P < .05$, *** $P < .01$).

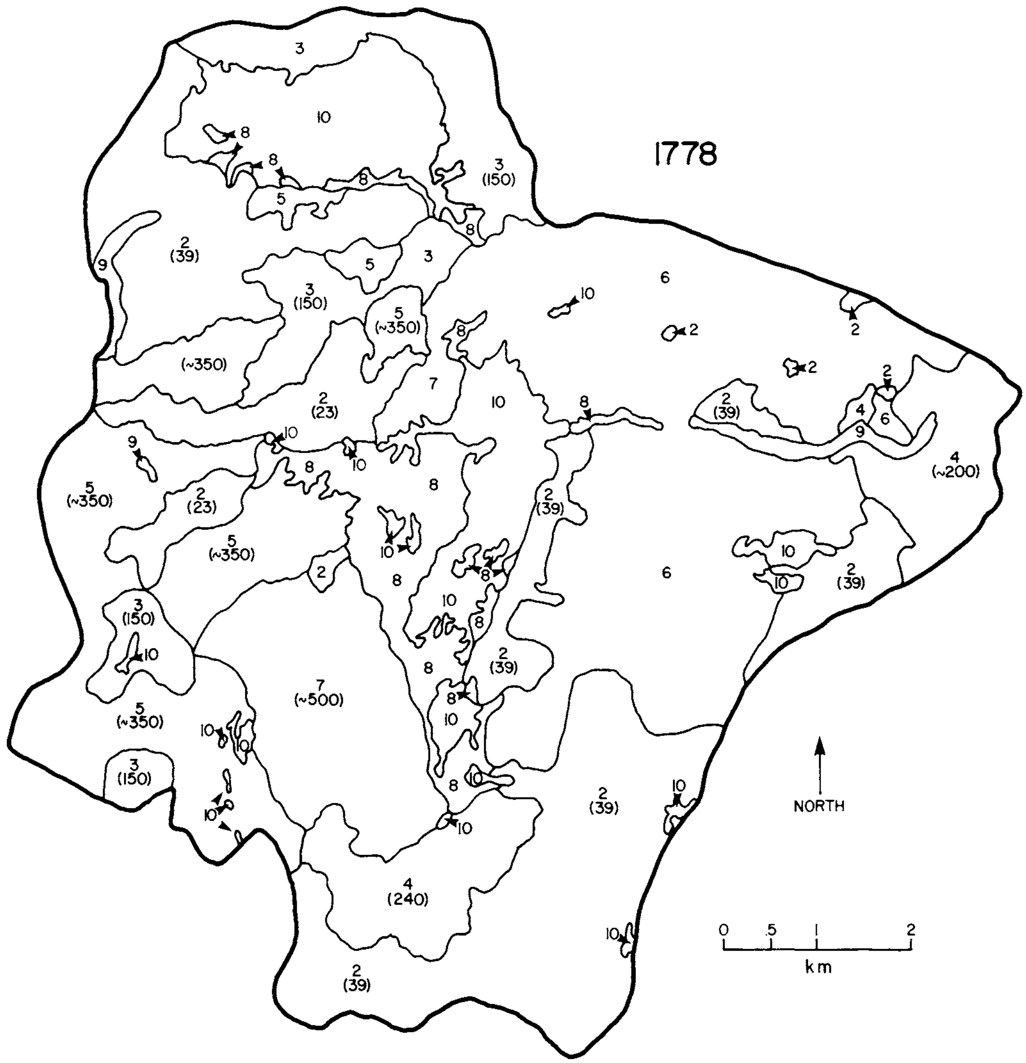


FIG. 7. Reconstruction of community types and stand ages (in parentheses) in the Little Firehole River watershed in 1778. The precise stand age could not be estimated in areas that were later burned. However, evidence indicates that these areas must have been in climax forest stages when they burned (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: Appendix 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 Abla/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 ≈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 Abla/Vasc habitat types under a natural fire regime. Major patterns are similar in the two habitat types except that changes in the Abla/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 Abla/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

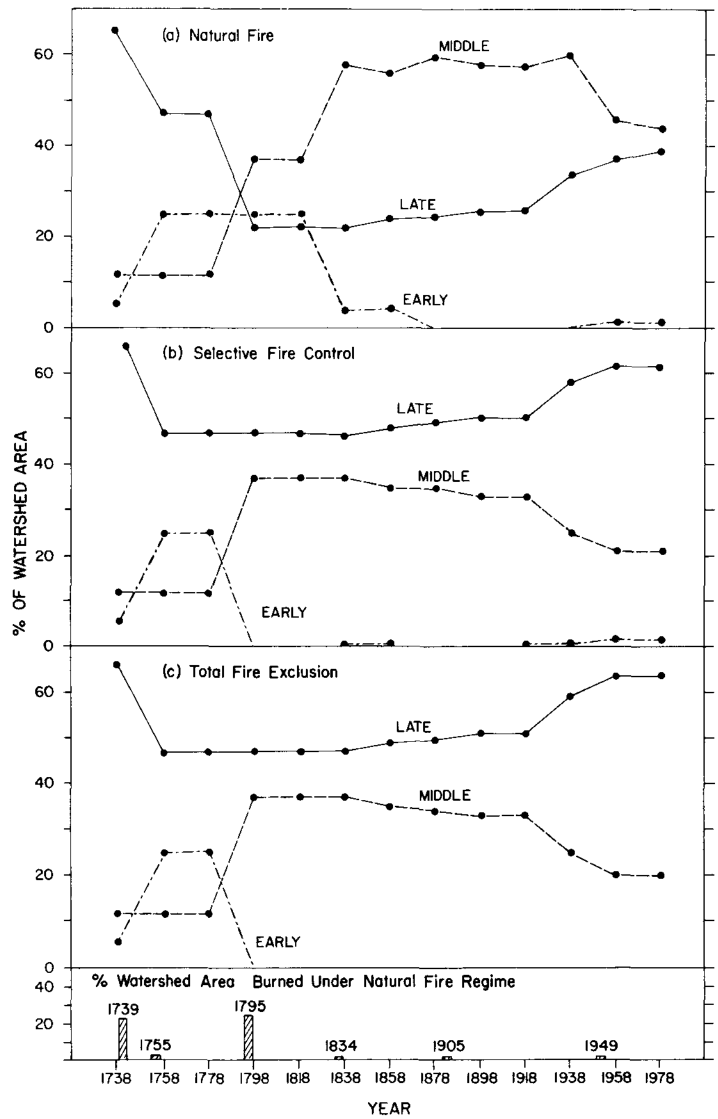


FIG. 8. Percent of area in the Little Firehole River watershed covered by early, middle, and late forest successional stages since 1738 under three different simulated fire regimes: (a) natural fire—all fires allowed to burn, (b) selective fire control—large fires excluded, small fires allowed to burn,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

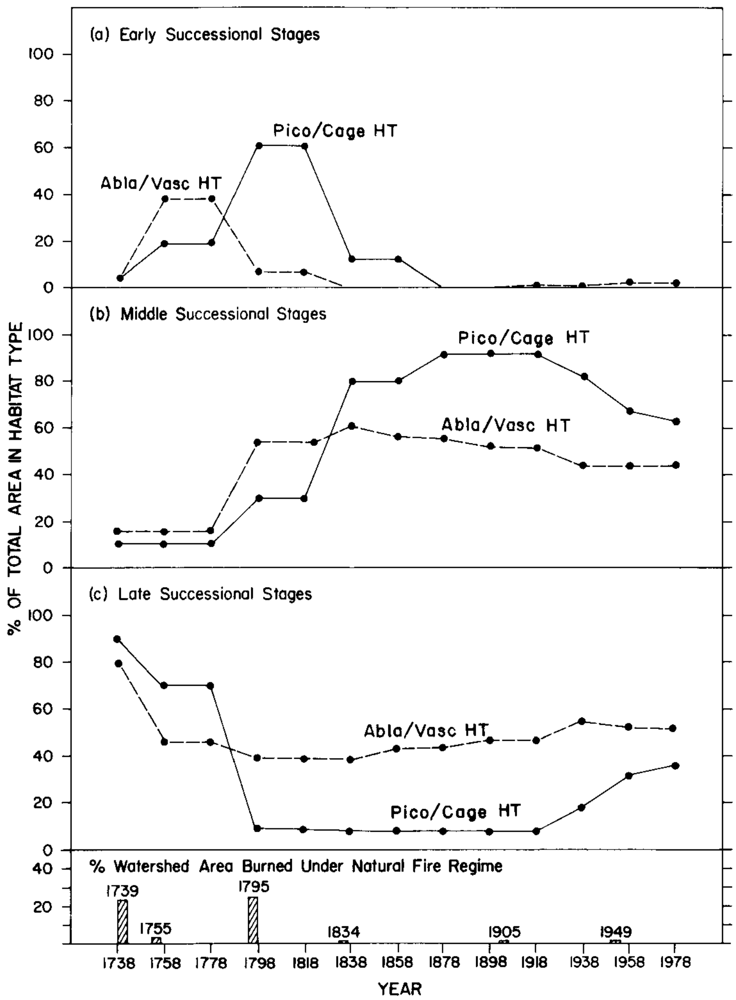


FIG. 9. Percent of area in the Pico/Cage and Abla/Vasc habitat types (HT) covered by early, middle, and late forest successional stages since 1738 under a natural fire regime.

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 surprising, 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

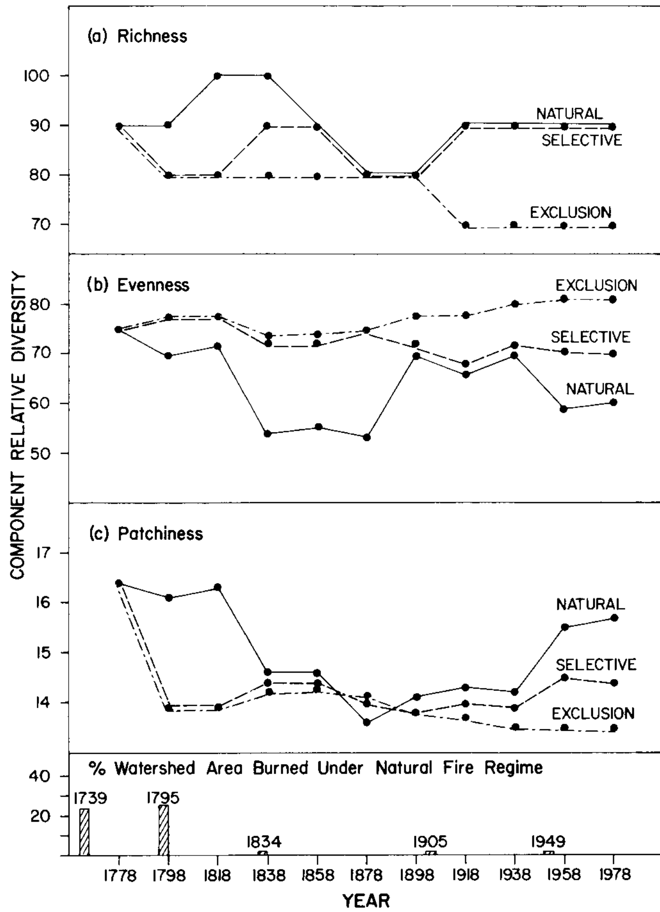


FIG. 10. Relative richness, relative evenness, and relative patchiness in the Little Firehole River watershed since 1778 under three different simulated fire regimes: (a) natural fire—all fires allowed to burn, (b) selective fire control—large fires excluded, small fires allowed to burn, and (c) total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

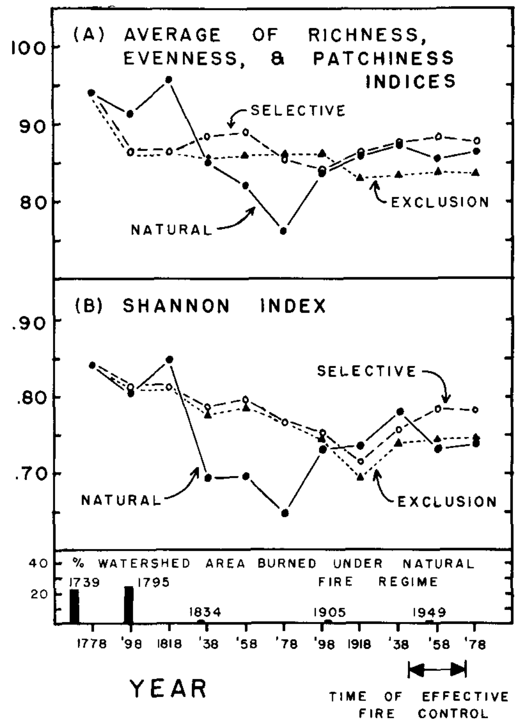


FIG. 11. Overall landscape diversity in the Little Firehole River watershed since 1778, expressed as: (A) a weighted average of the relative richness, relative evenness, and relative patchiness indices, and (B) the Shanon (Shannon-Wiener) Index ($H'$).

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 neither 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 ($\approx$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, $\approx$80 km south of the Yellowstone Plateau, and 500 m lower in elevation. A major fire there in August 1981, burned intensely in a 100-yr-old forest that had been affected by a severe outbreak of mountain pine beetles 20 yr earlier. I observed that the understory and fuel conditions in this forest resembled those of a 300-yr-old stand on the Yellowstone Plateau, apparently due to more favorable growing conditions and significant insect-caused mortality in the canopy of the younger stand. In contrast, lodgepole pine forests growing on poor soils at high elevations in the Wind River Mountains ($\approx$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-km$^2$ 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-km$^2$ watershed, due to the very large scale of fire-induced disturbance. For the purposes of management and interpretation 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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