

FIRE AND LANDSCAPE DIVERSITY
IN SUBALPINE FORESTS OF
YELLOWSTONE NATIONAL PARK

by

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A Thesis

Submitted to the

Department of Botany and

The Graduate School of the University

of Wyoming in Partial Fulfillment of Requirements

for the degree of

Doctor of Philosophy

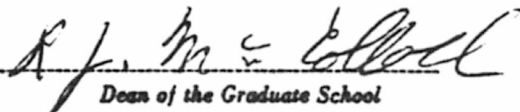
University of Wyoming

Laramie, Wyoming

December, 1979

*This thesis, having been approved by the
special Faculty Committee, is accepted
by the Graduate School of the
University of Wyoming
in partial fulfillment of the requirements
for the degree of*

Doctor of Philosophy


Dean of the Graduate School

Date December 1979

Romme, William H., Fire and Landscape Diversity in Subalpine Forests of Yellowstone National Park, Ph.D., Department of Botany, December, 1979

Fire history was documented using tree-ring analysis on a 73-km² subalpine watershed in Yellowstone National Park. Evidence was found for 15 fires since 1600, of which seven were major fires that burned >4 ha, destroyed the existing forest, and initiated secondary succession. Two major fires in the middle and late 1700's together burned half of the Watershed, the other fires being comparatively small. Fire frequency in this area is controlled by changes in the fuel complex during succession. Fuels capable of supporting a major 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 4 ha. Thereafter the occurrence of a destructive fire depends on the simultaneous occurrence of an ignition source and warm, dry, windy weather. On the extensive subalpine plateaus of Yellowstone National Park there appears to be a natural 300-400-yr fire cycle 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 during forest succession. The 73-km² study area currently appears to be about midway between major fire events in this cycle. This, rather than human fire suppression, apparently accounts for the small number and size of fires in the area during the last 150 yr.

Based on the fire history data, the sequence of vegetation mosaics covering the Watershed during the last 200 yr was reconstructed. 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 two 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 "non-steady-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 may be an important consideration in judging whether recent ecological changes are natural or man-induced.

The landscape reconstructions were repeated using a simulation model and hypothetical fire management policies of total fire exclusion and selective fire control (permitting only small fires to burn). The principle effect of both hypothetical fire regimes was to reduce the magnitude of periodic fluctuations in landscape diversity, resulting in more constant landscape composition over time. This difference may have implications regarding wildlife habitat and other ecological characteristics.

ACKNOWLEDGMENTS

This research was supported by a grant from the University of Wyoming - National Park Service Research Center. I also wish to thank several individuals whose assistance made the work possible. Dennis Knight, thesis director, reviewed early versions of the research proposal and final manuscript, as well as offering assistance and suggestions throughout the project. Mark Boyce, Martha Christensen, Don Despain, Nancy Stanton, and William Smith served as thesis committee members. Boyce and Stanton also gave suggestions on the selection of diversity indices; Despain offered provocative ideas on interpretation of the fire-scar record and freely shared his extensive observations of uncontrolled fires in Yellowstone National Park; Christensen assisted in evaluating the unknown cause of lodgepole pine mortality; and Smith gave suggestions regarding design of the computer simulation model. Yellowstone National Park Biologists Don Despain, Douglas Houston, and Mary Meagher, as well as the staff of the Old Faithful Ranger Station, arranged for lengthy stays in the backcountry, provided aerial photographs, and gave advice and encouragement throughout the study. James Brown of the U.S. Forest Service Northern Forest Fire Laboratory kindly applied my fuels data to the Rothermel computer-based fire behavior simulation model. Stephen Arno, also in the U.S. Forest Service, shared his experience in identifying and interpreting fire scars

in the field. Richard Levinson and Ronald Marrs of the University of Wyoming Remote Sensing Laboratory provided equipment and assistance in interpretation of aerial photography. Michael Cook gave suggestions and a critical evaluation of my computer simulation model. Lyman McDonald provided advice on the statistical analysis of the fuels data. Kenneth Diem of the University of Wyoming - National Park Service Research Program arranged for use of a house trailer in Yellowstone National Park during field seasons. Finally, I especially thank Richard Levinson, Larry Van Dusen, Kathleen White, and Philip White for their unfailing assistance and companionship during the long days, hard work, snowstorms, mosquitoes, and grizzly bears that accompanied our collection of fire history data in the Yellowstone backcountry.

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INTRODUCTION

The measurement and interpretation of diversity have been of interest to biologists for many years. Most work has focused on the diversity of species in communities, but, as Pielou (1975) points out, diversity exists and can be treated at many levels of biological organization. In this paper I present an analysis of vegetation diversity at the landscape level, i.e. the diversity of plant communities comprising the landscape of a 73-km² watershed in Yellowstone National Park. 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 (cf Reiners and Lang 1979). The relative contribution of these two kinds of patterns to overall landscape diversity varies, e.g., from desert mountain ranges where pronounced resource gradients control community composition and distribution (Whittaker and Niering 1965) to landscapes having a comparatively uniform abiotic environment where periodic fire maintains a

mosaic of successional stages (Heinselman 1973, 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). The richness of a landscape can be defined simply as the number of different community-types present, including community-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. A problem with most diversity indices is that every taxon is assumed to be equally different or distinct (Pielou 1975). Thus a landscape composed of an equal mixture of forest and grassland would have the same richness and evenness as a landscape with an equal amount of two forest types, two equally abundant taxa being present in each case. Yet intuitively the first landscape with more dissimilar communities seems more varied than the second. Another consideration unique to landscape diversity is the size and interspersion of individual community units, a landscape with three community-types distributed in many small patches appearing more diverse than a landscape with the same three community-types in a few large blocks. To resolve both problems I calculated a third diversity component related to the interspersion and contrast of communities -- a "patchiness component". I examined richness, evenness, and patchiness and then combined them for an overall index of landscape diversity.

As with species diversity, landscape diversity is intrinsically interesting. However, the major reason for measuring diversity at any level of organization is to judge its relationships to other structural and functional properties of the system (Pielou 1975). Over 45 yr ago Aldo Leopold (1933) recognized the connection between landscape diversity and wildlife habitat in his law of interspersion: "the potential density of game ... requiring two or more [plant community] types is ... proportional to the sum of type peripheries." Since then wildlife biologists have been concerned with concepts of habitat diversity and "edge" (Patton 1975), with recent research increasingly focused on quantifying the proportions and spatial arrangements of plant communities comprising optimal habitat for a species or group of species (Myers and Morris 1975, Lyon 1976, Thomas et al. 1976). Recent studies also have shown a relationship between landscape diversity and hydrologic processes. Converting patches of a forested watershed to earlier successional stages through timber harvest may change patterns of snow accumulation and melt (Leaf 1975) and may increase total stream discharge (Rich and Gottfried 1976, Jaynes 1978). Loucks (1970) showed that primary production and tree seedling diversity were highest during intermediate forest successional stages, and predicted a decline in overall diversity and production if man causes unnaturally large portions of the landscape to be covered by late successional forests. In addition to describing landscape diversity patterns in Yellowstone National Park, I will discuss possible implications to the wildlife, hydrology, and total biotic diversity of the Park.

Where fire has been an important natural disturbance under primeval conditions, particularly in wilderness areas, parks, and other natural areas, 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 post-fire successional stages appears to have declined in some areas, with older stages increasingly dominating the landscape (Habeck 1970, Habeck and Mutch 1973). This concern is a major impetus for the current development of new fire management plans that are returning fire to the system either by permitting some lightning-caused fires to burn or 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 re-introduced 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. 1977). My approach in Yellowstone National Park 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, this study entailed (1) the documentation of fire history and the rates and patterns of forest succession following fire, with this information being used to reconstruct the vegetation mosaics that must have existed in the past as well as to project with computer simulation the future mosaics that would probably develop under different fire regimes; and (2) a quantitative measure of landscape diversity at each point in the temporal sequence so produced. Yellowstone National Park provided an ideal site for studying natural long-term vegetation patterns because it contains large areas relatively free of human influence.

Several different aspects of fire history were important in this study. Fire incidence (the number of fires occurring per unit area per time) and the total area burned by each fire were determined by fire-scar analysis, while an estimate of fire frequency (the interval between successive fires on a single site) was made following a synthesis of all available data. Despain and Sellers (1977) hypothesized that fire frequency in this area is controlled by the gradual development during succession of a fuel complex capable of supporting a hot fire. To test this hypothesis I sampled fuels in a chronosequence of stands ranging from early to late

successional stages. The mountain pine beetle (Dendroctonus ponderosae Hopkins) also appears to influence fire cycles by accelerating the accumulation of dead, woody fuels (Amman 1977); I incorporated this effect into my fire frequency analysis also.

STUDY AREA

The study was conducted on the 73-km² Little Firehole River Watershed located west of Old Faithful on the Madison Plateau, a relatively flat Quarternary lava flow covering several hundred km² in west - central Yellowstone National Park. Plateau rhyolite forms the bedrock throughout, being covered by sandy glacial till and kame deposits on the uplands and fine-grained alluvium along streams and moist meadows (U.S. Geological Survey 1972a,b). With the exception of a deep canyon cut by the Little Firehole River, the eastern and northern portions of the watershed have relatively little topographic relief, with small hills and depressions typical of kame topography and an average elevation of 2450-2500 m. 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 on this watershed afforded a good opportunity to study long-term fire cycles as affected primarily by patterns in 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 about 102 cm annually in the eastern and northern portions of the watershed to

about 152 cm in the southern and western parts. Most of the area receives ca 125 cm annually (mainly as winter snow), which is 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 night-time frosts. Prevailing winds are from the southwest.

Three major habitat-types¹ (Steele et al. 1977) are found in the study area, a habitat-type being an aggregation of land units capable of producing similar climax vegetation and named after the dominant climax tree and a dominant or characteristic herb or shrub. In the Pinus contorta/Carex geyeri (Pico/Cage) habitat-type, which covers ca 25 km² in the drier eastern and northern portions of the watershed, lodgepole pine (Pinus contorta var. latifolia Engelm.) dominates both pioneer and climax forest stages. Lodgepole pine also dominates early successional stages in the Abies lasiocarpa/Vaccinium scoparium (Abla/Vasc) habitat-type (covering ca 36 km² in the more mesic western and southern areas) but shares dominance with subalpine fir (Abies lasiocarpa (Hook.) Nutt.), Engelmann spruce (Picea engelmannii Parry), and whitebark pine (Pinus albicaulis Engelm.) in the climax. The Abies lasiocarpa/Calamagrostis canadensis (Abla/Caca) habitat-type covers ca 4 km² on moist, alluvial sites along streams and meadows, being characterized usually by a dominant lodgepole pine canopy and a rich herbaceous ground cover. Spruce

¹Modified slightly from Steele et al.(1977)

and fir invade this habitat-type, through lodgepole pine appears to remain as a co-dominant (In contrast to some other parts of the Rocky Mountains where riparian sites support spruce-fir forest (Romme 1977, Whipple and Dix 1979)).

Post-fire succession is similar in the two upland habitat-types (Pico/Cage and Abia/Vasc), with the successional continuum divisible into six relatively distinct stages (modified from Despain 1977) which constitute some of the taxa that I treated in the analysis of landscape diversity (see also App. 4 and Table 1). The initial herbaceous stage 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, with the herbs remaining abundant until canopy closure, after which herbaceous production and diversity decline sharply (Taylor 1969). Most of the pine usually become established during the first several years to form a dominant, even-aged cohort, with reduced pine establishment thereafter due to the species' shade intolerance (Tackle 1959). Large standing and fallen fire-killed stems remain prominent throughout this stage, with small dead woody material still sparse.

The third successional stage, including the time from initial canopy closure to maturation of the even-aged pine cohort, is

Table 1. Age intervals for the 10 community-types identified on the Little Firehole River Watershed.

Those types with no interval given are believed to change much more slowly and were treated as static entities for the purposes of this study.

COMMUNITY TYPE	Pico/Cage Habitat-type				Abla/Vasc Habitat-type		
	Typical stands	Early pine canopy mortality	Late pine canopy mortality	Slow restocking	Typical stands	Early pine canopy mortality	Late pine canopy mortality
1. Herbaceous stage	0-20	0-20	0-20	0-40	0-20	0-20	0-20
2. Seedling-sapling stage	20-40	20-40	20-40	40-80	20-40	20-40	20-40
3. Immature pine forest stage	40-150	40-150	40-150	80-200	40-150	40-150	40-150
4. Mature pine forest stage	150-200	150-170	150-300	200-250	150-300	150-180	150-350
5. Transitional stage	200-300	170-240	300-400	250-350	300-400	180-280	350-450
6. Climax forest: Pico/Cage HT	300+	240+	400+	350+			
7. Climax forest: Abla/Vasc HT					400+	280+	450+
8. Riparian forest: Abla/Caca HT							
9. Steep slope forest							
10. Meadow							

characterized by rapid tree growth and extensive self-pruning of lower limbs plus thinning in dense stands. Most of the large fire-killed stems fall and decompose during this time, with duff and litter beginning to accumulate on the forest floor. 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, a sparse understory of fir and spruce beginning to develop on sites capable of supporting these shade-tolerant species. Annual wood increments in the dominant pine are very small.

Extensive mortality eventually begins to occur in the even-aged pine canopy, marking the onset of the fifth successional stage. In the Abia/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 standing and fallen large, dead stems.

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, and stand

structure and composition appear to remain relatively constant until the next major disturbance.

No clear successional patterns are evident in the riparian Abia/Caca habitat-type. Because this forest type covers a relatively small area, with fire apparently being less frequent and destructive than in the drier upland forest types, I treated it as a single, constant community-type in my analysis of landscape diversity. Two additional community-types that apparently change little with time are subalpine meadows and the sparse forests of pine, fir, and spruce on steep, rocky slopes.

By combining the habitat-types and successional stages occurring on the Little Firehole River Watershed I produced the community-type classification shown in Table 1. Cluster analysis of structural characteristics in 18 stands supports this classification (App. 4). With the exception of the climax stages there is little difference in appearance or structure between the Pico/Cage and Abia/Vasc habitat-types. Though herbaceous species composition may differ somewhat in earlier successional stages, 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). The two climax forests appear significantly different in structure and function, however, and are classified as distinct communities.

The rate of succession varies in response to local site conditions and disturbance history, the seral stage endpoints shown in Table 1 being based on extensive observation of stands of different ages and successional stages 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. Tree age data from this study show that the initial, even-aged lodgepole pine cohort usually became established within the first several years after a fire. 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, Habeck 1970), herbaceous competition (Stahelin 1943, Langenheim 1963), or inadequate seed source, most cones in this area being non-serotinous.

The onset of extensive mortality in the even-aged pine canopy is generally earlier in the Pico/Cage habitat-type than in the Abia/Vasc habitat-type, due to the effects of the mountain pine beetle 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 being most vulnerable (Amman et al. 1977). Beetles sometimes cause early canopy mortality in the more mesic Abia/Vasc habitat-type, but their effect is most widespread in the Pico/Cage habitat-type where the mature pine forest stage (Table 1) usually lasts only a few decades

compared to a century or more on other sites. Observations of recently killed trees indicate that a low to moderate beetle population presently exists in the Pico/Cage habitat-type on 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, probably the result of pine beetle damage.

The second type of early canopy mortality (the cause unknown at this time) in the Pico/Cage habitat-type occurs in localized but widespread patches, usually of a hectare or less and most often in dense stands on dry sites. Small as well as large canopy trees are killed, whereas the pine beetle kills only larger trees. The bark on the lowermost 1-2 m of stem in affected trees appears to first separate from the wood, later to crack and peel away. Eventually the tree dies after the bark has been lost around the entire circumference. Some trees have similar lesions near the top of the stem, but in most the damage is confined to the base. 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).

Human disturbance on 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. Archaeological studies in Yellowstone National Park (Taylor 1964) show that pre-historic man was present in the geyser basins a few km 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 the Park's establishment in 1872, 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. 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 (U. S. National Park Service 1975).

METHODS

Fire History

The incidence and areal extent of past fires was determined using fire-scar methods developed by Arno and Sneek (1977) and Heinselman (1973). Living fire-scarred trees were located and sectioned with a 3-foot bow saw. An attempt was made to date fire scars with an increment corer, but only very approximate dates (± 20 years) could be obtained. Lodgepole and whitebark pine with single fire scars were found frequently, with multi-scarred trees being less common. Care was taken to distinguish fire scars from scrape scars, bear-feeding scars, and other forms of injury (Molnor and McMinn 1960). To test the accuracy of the method, fire scars also were taken from two areas known to have burned in 1901 and 1949.

In the laboratory the fire-scar sections were sanded, wetted, and the rings counted under a 10X 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. This problem, plus the difficulty of determining the exact fire annulus in some sections, resulted in some dating errors. In general, fire years reported here within the last 100 years are ± 2 yr; between 100-200 yr ago, ± 3 yr; and over 200 yr ago, ± 5 yr. After analyzing the fire-scar sections a fire chronology was constructed as described in Results.

In addition to sampling fire-scarred trees, increment cores were taken from several dominant lodgepole pine to document post-fire reproduction, lodgepole pine being the major shade-intolerant species restocking recently-burned sites in this area. Dominant trees appeared to have been unsuppressed throughout their lives and generally were the largest individuals. Cores were taken as close to the base as possible, with an estimate of age at coring height added to the number of rings on the core. Dominant Engelmann spruce, whitebark pine, or subalpine fir were aged in some late-successional stands. Fire-scar sections and/or increment cores were obtained in 92 stands distributed throughout the watershed (App. 1). 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 (ETZ series, 1969, 1971) to a basemap using a zoom-transfer-scope. Stands differing in age by more than 100 years 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 (Levinson and Marrs 1978). 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 40-80, with most between 50-60), but stand age was not correlated with these factors (Fig. 2-6, 2-7; App. 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 or planes were counted in each stand, resulting in percent errors (standard error divided by $\bar{x}$ times 100) of about 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). In addition, site index, a relative measure of potential site productivity which is expressed as the average height (in feet) of dominant trees at age 100 years, was determined directly in lodgepole pine-dominated stands 30-200 years old (Alexander 1966). In stands outside this age-range an estimate of site index was obtained by assigning the value of a nearby stand on 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

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

FUEL CATEGORY	UNITS	DESCRIPTION	MAJOR EFFECT ON FIRE BEHAVIOR
Needle Litter	mm	Undecomposed needles, twigs, cone scales, and other small particles on the ground	Fuels supporting ignition and initial surface spread
1-Hour Timelag Fuels (1-HR TL)	kg/ha	Dead, woody pieces <u><</u> 0.635 cm diameter	

Total Fuels	kg/ha	Dead, woody pieces of all sizes	Fuels con- tributing to intensity (heat release) and flame height

1000-Hour Timelag Rotten Fuels (1000-HR TL ROTTEN)	kg/ha	Dead, woody pieces >7.6 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	

of a forest stand that could be expected to produce such a change, the relationship of fuels to stand age was analyzed 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 in fact shows this pattern. A step-wise linear regression was performed for each stand-age interval, fuels (kg/ha) being the dependent variable and stand age and site index being the two independent variables. Where a significantly non-zero 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 non-zero or where site index accounted for most of the variation, no change in fuels attributable to stand age was assumed. Bevins et al. (1977) constructed a model for lodgepole pine forests in southern Montana which predicts fuel mass at any given stand age using polynomial regression analysis and a large database. A predictive model of this sort is not feasible with the smaller amount of data in the present study, however, and significant general trends are emphasized instead.

Fuels data from two representative stands in the Pico/Cage and Abia/Vasc habitat-types on the Little Firehole River Watershed, 350 yr and 450 yr old respectively, were applied to Rothermel's (1972) computer-based fire behavior simulation model with the

assistance of the USDA Forest Service Northern Forest Fire Laboratory in Missoula, Montana. This model predicts fire intensity and rate of spread based on the weight and moisture content of small dead woody fuels (<7.5 cm diameter), needle litter, and live fuels. The model is limited by its assumptions of a homogeneous fuel bed and non-crowning 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, Houston 1976). Such historical documentation was not available for the Little Firehole River Watershed, however 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 recreate 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 on 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 (Houston 1976), 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). There is evidence that destructive fires in the subalpine forests of Yellowstone Park occur primarily in late successional stands, the younger stands lacking the combination of fuel characteristics necessary to support an intense fire (see Results - Fire History). Therefore, I assumed that each area was in the climax stage when it burned, an assumption supported by observations of recent, uncontrolled fires in the Park (Despain and Sellers 1977). However, it was impossible to know exactly how old a stand was when it burned, thus 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 that initially

recolonized the site as well as any fire-scarred trees have long since disappeared. Such areas comprise about 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 probably is 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 (Habeck 1970, 1976; Quirk and Sykes 1971; Romme 1977), 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 since the fuel characteristics in climax stands confer a high fire risk in an area where summer lightning storms are common. These stands generally are surrounded by younger stands of known age, usually separated by a sharp discontinuity. 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 due to changes in the fuel bed rather than wind, moisture, or other external factors (Despain and Sellers 1977). If it can be assumed that similar fire behavior in the past was responsible for the distinct forest discontinuities observable today, then most stands that are presently in a climax

stage must have been in an earlier stage at that time in the past when an intense fire burned to their borders and stopped. High fire risk develops around age 350 yr in forests of this area (see Discussion), 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 stand age today would be the average age at which stands on the type of site in question can be expected to first develop the characteristics of the climax stage. For each climax stand on non-topographically sheltered sites I assigned the mean of this maximum and minimum estimate as the stand age in 1978 and used it for reconstruction of past landscapes. No doubt there are errors in these estimates, but I believe they are of sufficient accuracy for my purposes.

The approach just described allows recreation 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 which simulates succession and periodically calculates landscape diversity indices. Regional models of eastern deciduous forest dynamics have been constructed for similar purposes (Shugart et al. 1973, Johnson and Sharpe 1976, Johnson 1977). These models simulate landscape changes based on transfer coefficients expressing the average proportion of each vegetation type (or successional stage) that changes into another type per unit of time, the transfer

coefficients being obtained from long-term permanent plot data. However, use of constant transfer coefficients was not appropriate in my much smaller study area where fire has created large blocks of even-aged forest. Because all stands in each even-aged block undergo successional development more-or-less in unison, there is no conversion from one type to another for many years, followed by very extensive conversions during a short time period.

Therefore, I used a different approach in which I divided the 73-km² watershed into 1429 5-ha cells, constructed a basic model of forest succession, and applied it to each cell individually. Every cell was first assigned a habitat type, an initial stand age, and a set of ages representing seral stage endpoints (Table 1), these data being empirical and based on the location of the cell on the watershed. An algorithm then determined the state of each cell, i.e. to which of ten community-types it belonged (Table 1). Cells in the upland forest habitat types were classified according to stand age as one of seven community-types representing successional stages, the other three community-types representing habitat-types in which community structure and composition remain relatively constant over time. 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 as many times as desired. 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 App. 3 for programming details).

Quantitative Landscape Diversity Indices

A bewildering assortment of quantitative indices for measuring biological diversity has been proposed, each having certain advantages and disadvantages for a particular situation (Peet 1974). Rather than offer additional indices for measuring landscape diversity, I have attempted to select existing indices that most appropriately describe diversity at the landscape level, making slight modifications only when necessary. There probably is no single "best" diversity index. Each conveys somewhat different information about the entity being measured, and therefore I measured landscape diversity in several different ways.

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 different community-types present and divided by 10, which is the total number of taxa recognized in the study (Table 1). To measure evenness I selected 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. Simpson's index is most sensitive to increases in one

Table 3. Landscape diversity indices (see text).

I. Relative Richness (R)

$$R = \frac{T}{10} \times 100$$

where T = number of different
community-types
present (maximum
possible number is 10)

II. 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

H2(max) = maximum
possible value
of modified
Simpson's index

p_i = proportion of total
landscape area
covered by i^{th}
community-type

T = number of different
community-types
present

III. Relative Patchiness (P)

$$P = \frac{\sum_{i=1}^N C_i}{\sum_{i=1}^N C_{max}} \times 100$$

where N = number of 5-ha cells
comprising the
landscape

C_i = contrast between
the i^{th} cell and its
adjacent neighbor

C_{max} = maximum possible
contrast between
adjacent cells

IV. Overall Landscape Diversity (D)

$$D = \frac{\frac{R}{R_{max}} + \frac{E}{E_{max}} + \frac{P}{P_{max}}}{3} \times 100$$

where R_{max} = maximum observed R

E_{max} = maximum observed E

P_{max} = maximum observed P

or a few predominant community-types (Peet 1974), whereas the richness index responds equally to the addition of new community-types whether they cover a large or small area.

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. In addition to the total amount of edge, indicated by Patton's index, I desired an expression of the degree of contrast between adjacent communities. For this I compared each 5-ha unit in the computer model to its adjacent neighbors, using a matrix of dissimilarity values ranging from 0.0 - 1.0 and based on qualitative differences in physical structure and species composition (Table 4). To calculate a patchiness index I summed the dissimilarity values for every pair of adjacent 5-ha units and divided by the maximum dissimilarity value that would exist if each unit were adjacent on all sides to a maximally different subunit (Table 3). Finally, I computed an overall landscape diversity index by standardizing the relative richness, evenness, and patchiness indices, thereby giving equal weight to each, and then averaging the three (Table 3).

The frequently-used Shannon-Wiener diversity index (Pielou 1975) is not appropriate for my analysis of landscape diversity because (1) it is based on sample data, whereas I conducted a complete census of stands on the watershed; and (2) it incorporates richness and evenness but omits the patchiness component which I

believe is an important part of landscape diversity. Pielou (1975) offers a "spatial diversity" index which incorporates a patchiness component, but it too is based on sample rather than census data.

The problem of classification, which bedevils nearly every attempt to measure diversity (Pielou 1975), is especially serious when the taxa being considered are nebulous "community-types" and arbitrarily defined stages in a successional continuum. The community is generally recognized as a functional entity, but the characterization and classification of distinct community-types is highly controversial. Thus a quantitative diversity index might have several different values for the same landscape depending on the classification system used. The community classification used in this study (Table 1) was based on easily recognized differences in structure, species composition, and habitat, and was supported by an objective classification technique (cluster analysis -- see App. 4).

RESULTS

Fire History

Table 5 presents a fire chronology for the Little Firehole River watershed, based on fire-year determinations from 44 fire-scarred trees in 36 stands (Appendix 1). Note that several fire years are represented by a cluster of sample dates, the variation being attributable to errors in ring counts. The actual fire year in these cases was estimated based on the frequency distribution of sample dates plus the age of post-fire lodgepole pine reproduction in affected stands. Using fire scars only, a total of 14 fires during the last 350 yr were documented, with an additional fire around 1630 being suggested by extensive 350-yr-old lodgepole pine stands. Of these 15 fires during the last 350 yr, 7 could be classed as major fires that covered 4 ha or more, destroying the existing forest and initiating secondary succession. The remaining 8 fires apparently covered very small areas and produced little change in the vegetation.

The fire-scar method appears to give reliable estimates of past fire years within the limitation of error in ring counts ($\pm 2-5$ yr). Each of three fire-scarred trees sampled in 1978 from an area known to have burned in 1949 had 29 annual rings between the fire annulus and cambium, giving a correct fire data of 1949.

Table 5. Fire years since 1600 on the 73-km² Little Firehole River Watershed. Major fires burned >4 ha, destroying the existing forest and initiating 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
ca 1932		X		ca 1932
1905	X		X	1905, 1907, ca 1912
ca 1890		X		ca 1888, ca 1889
ca 1881			X	ca 1881
ca 1860		X		ca 1858, ca 1859
ca 1851			X	ca 1851
1834	X	X		1834
ca 1827		X		ca 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, ca 1802
1755	X		X	1755
1739	X	X	X	1739, 1739, 1739, 1739, 1740, 1741, 1741, 1742, 1742, 1743, 1743, 1744, ca 1746
ca 1659		X		ca 1659
ca 1643		X		ca 1643
ca 1630	X	X	X	*

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

Similarly, 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) gave fire dates of 1900 and ca 1900, the rings being difficult to count in the latter.

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

$$\begin{aligned}\text{Incidence} &= (10-1) \text{ fires}/25.4 \text{ km}^2/302 \text{ yr} \\ &= .00117 \text{ fire/km}^2/\text{yr}\end{aligned}$$

The time period was the interval between the oldest and most recent documented fires, with the number of fires in the calculation being one less than the total number occurring during that time. 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; Despain, personal communication). Vegetation and climate here are similar to the Little Firehole River Watershed (Despain 1973). The two plateaus had five times as many fires (Table 6). This is to be expected since many prehistoric small fires on the Little Firehole River Watershed undoubtedly left no scarred trees or other evidence.

Table 6. Historical fire incidence on 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 Despain, personal communication). Major fires burned >4 ha, destroying the existing forest and initiating secondary succession.

	AREA (km ²)	ALL FIRES		MAJOR FIRES		FIRE INCIDENCE (fires/km ² /yr)	
		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	.00117	.00058
Abla/Vasc Habitat-type	36.1	1630-1949	8	1630-1949	6	.00061	.00043
Entire watershed	73.2	1630-1949	15	1630-1949	7	.00060	.00026
Two Ocean and Mirror Plateaus	1380	1972-1978	30	1972-1978	7	.00311	.00072

The record for major fires on the Little Firehole River Watershed is more complete, but again the incidence of major fires has been two to three times greater on the Two Ocean and Mirror Plateaus (Table 6). Although total fire incidence in the Pico/Cage habitat-type has been nearly twice that in the Abia/Vasc habitat-type on the Little Firehole River Watershed, the incidence of major fires has been approximately equal in the two habitat-types (Table 6).

Figure 1 shows the sizes of all documented major fires since 1600 in the Pico/Cage habitat-type, Abia/Vasc habitat-type, and entire Little Firehole River Watershed. The areas are expressed as percent of total area rather than km^2 because several fires also burned adjacent areas outside the Watershed and their total size unknown. Although the incidence of major fires has been approximately equal in the two upland forest habitat-types (Table 6), more area has burned in the Pico/Cage habitat-type, over 90% compared to only 55% in the Abia/Vasc habitat-type (Fig. 1). This difference is probably due to the fact that the Abia/Vasc habitat-type occurs in the western and southern portions of the Watershed where elevation and precipitation are higher. A climax spruce-fir forest covering about 1.5 km^2 on a northeast-facing slope between 2450-2550 m was estimated to be more than 550 yr old, several spruce and pine >500 yr old being found. This site, topographically sheltered from the prevailing southwest wind, probably burns very rarely.

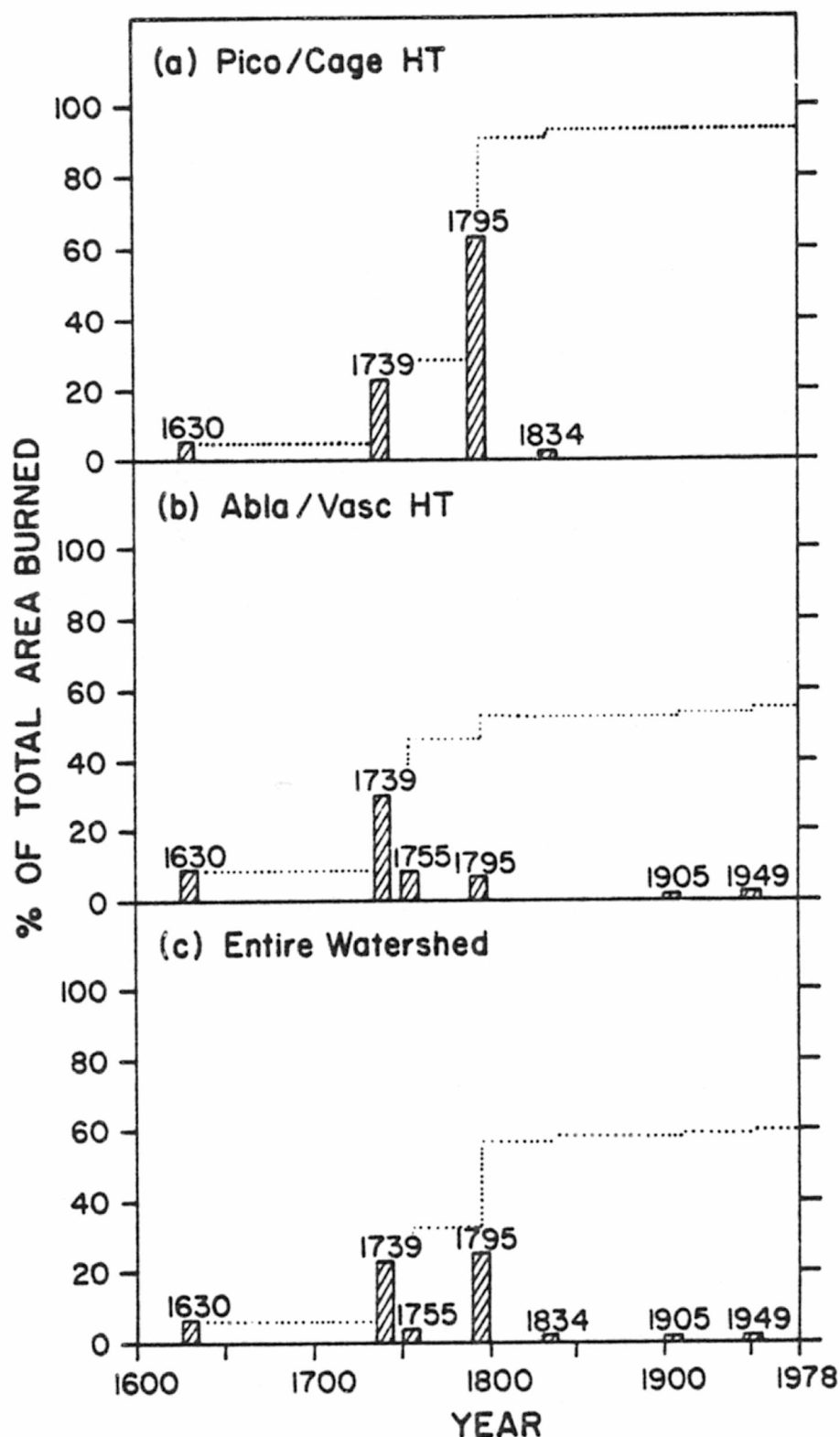


Figure 1. Sizes of documented major fires since 1600 in the Pico/Cage habitat-type (HT), Abia/Vasc HT, and entire Little Firehole River Watershed, expressed as percent of total area in the habitat-type or Watershed, respectively. The dotted line shows the cumulative area burned since 1600.

Several kinds of evidence indicate that fires covering large areas on the Little Firehole River Watershed were chiefly destructive, standing-replacing burns, with the extensive, low-intensity, non-stand-replacing burns reported for subalpine forests in the northern Rocky Mountains (Arno 1976, Gabriel 1977, Sneck 1977, Tande 1977) apparently being of minor importance here. This interpretation is supported by the fact that fire-scarred trees were usually found in clumps and rarely had more than a single fire scar, indicating that they represented the margins of destructive burns or islands of unburned trees within a burned area. Furthermore, nearly all lodgepole pine stands were found to be 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; Despain, personal communication). Only a very small portion of the Watershed (<5%) has burned more than once during the last 350 yr, chiefly along boundaries between two burns where the second fire apparently burned a short distance into the area burned earlier before going out.

Fuel Accumulation

Small fuels capable of supporting fire ignition and initial spread (needle litter and 1-HR 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. 2). Small fuels remain constant or decrease slightly in later stages as production of small materials declines and is balanced by decomposition. 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 carry a fast-moving surface fire. Using my data for a 350-yr-old and 450-yr-old stand (App. 2), 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 60-87 kcal/sec/m of fireline, respectively. 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. 3). The developing even-aged pine forest subsequently 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 about 70-200 yr. Total fuels then begin to increase with the onset of extensive mortality in the even-aged pine 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

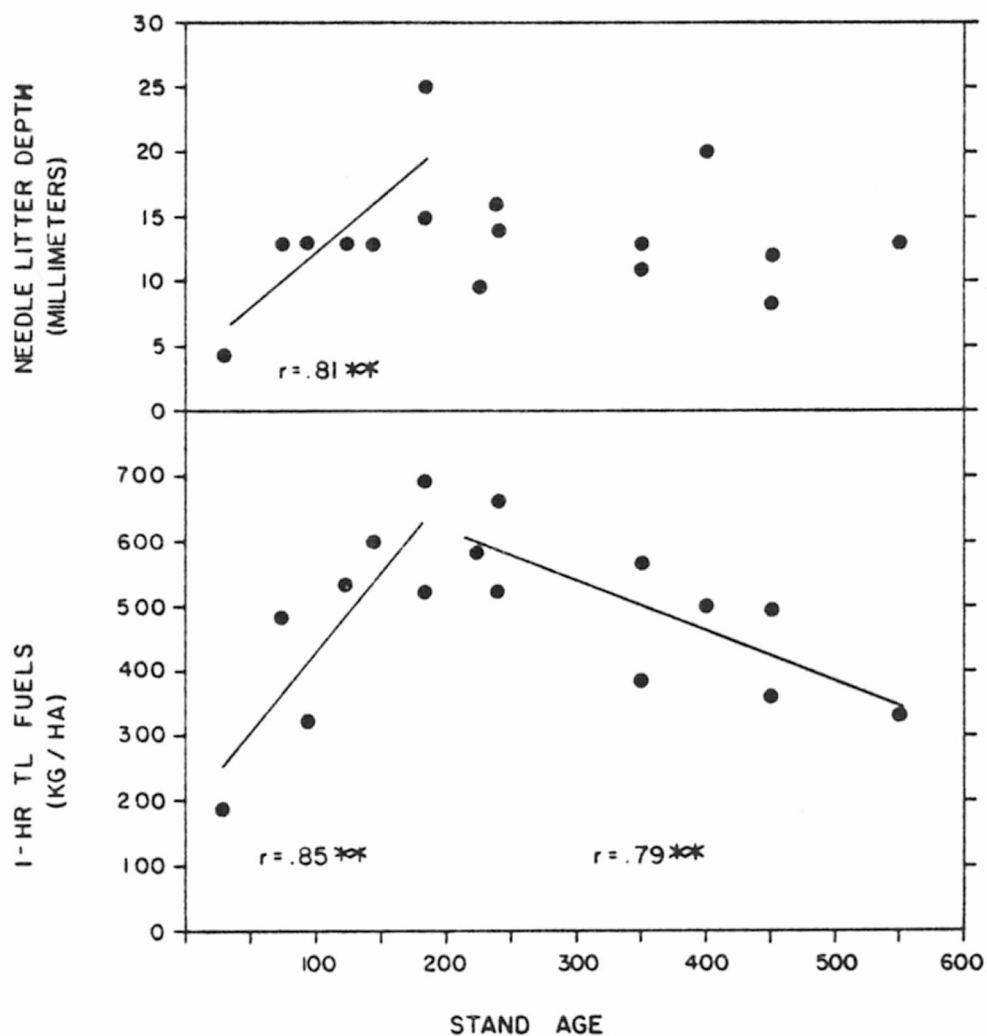


Figure 2. Changes in small fuels capable of supporting ignition and initial fire spread along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (** = 95% significance level).

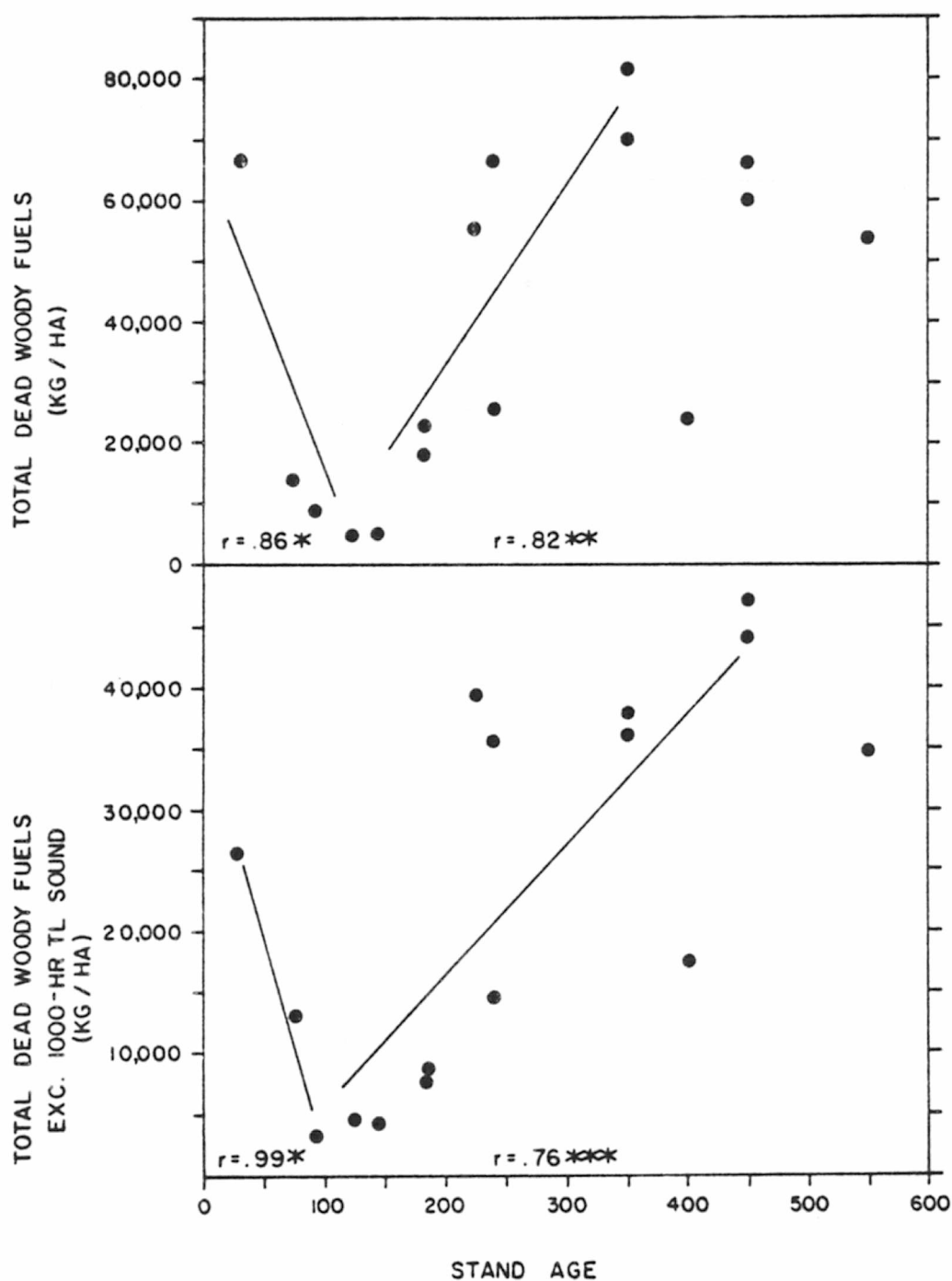


Figure 3. Changes in total dead woody fuels and total fuels excluding 1000-HR TL sound fuels along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (* = 90% significance level; ** = 95%; *** = 99%).

sound material up to about 7.5 cm diameter is actually combusted during intense fires in Yellowstone National Park (D. G. Despain, personal communication). However, the larger sound material (1000-HR TL fuel) which 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 excluding the relatively non-combustible 1000-HR TL sound fuels (i.e., all rotten material plus sound pieces <7.5 cm diameter), observing the same general pattern except that maximum fuel accumulations occur later, around 450 yr (Fig. 3).

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 occurring 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 Figure 4 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 due to the small amount of fine fuels present. Subsequent self-pruning by maturing lodgepole pine eventually creates a gap between the lowermost branches and the ground. In a mature pine forest (ca 200 yr old) this space may be 3 m or more and filled only by relatively non-flammable

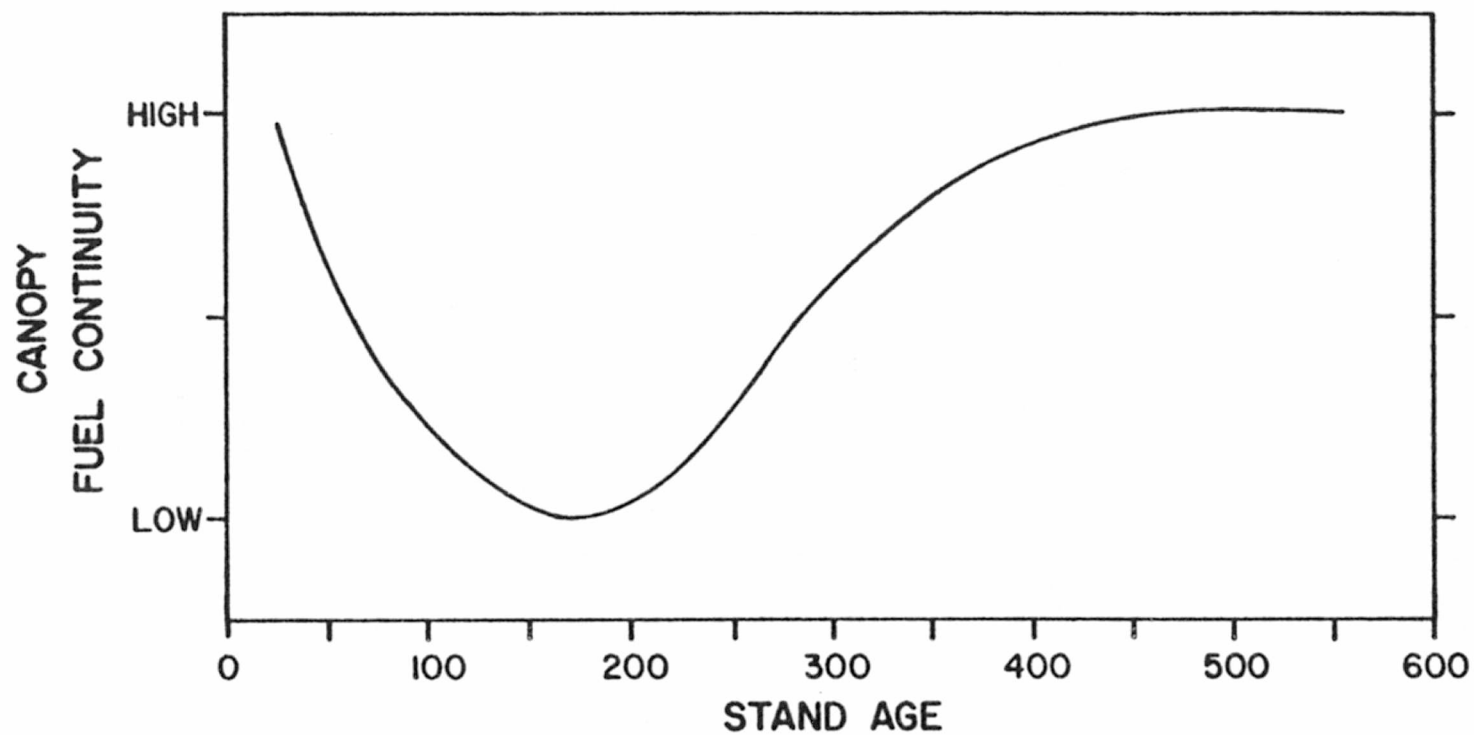


Figure 4. Qualitative changes in canopy fuel continuity along a chronosequence of upland forest stands.

large tree trunks. At about the time the even-aged lodgepole pine forest begins to break up with natural mortality (ca 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 the lower branches throughout their lives, create relatively greater vertical continuity than small lodgepole and whitebark pine 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 (ca 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 (ca 400 yr) however, both vertical and horizontal canopy continuity appear adequate to support an intense crown fire (Fig. 4).

Fuels in which a fire may smolder and persist during cool, humid, or rainy periods (1000-HR TL rotten fuels and duff) are generally low during early and middle successional stages but increase in later stages (Fig. 5). 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

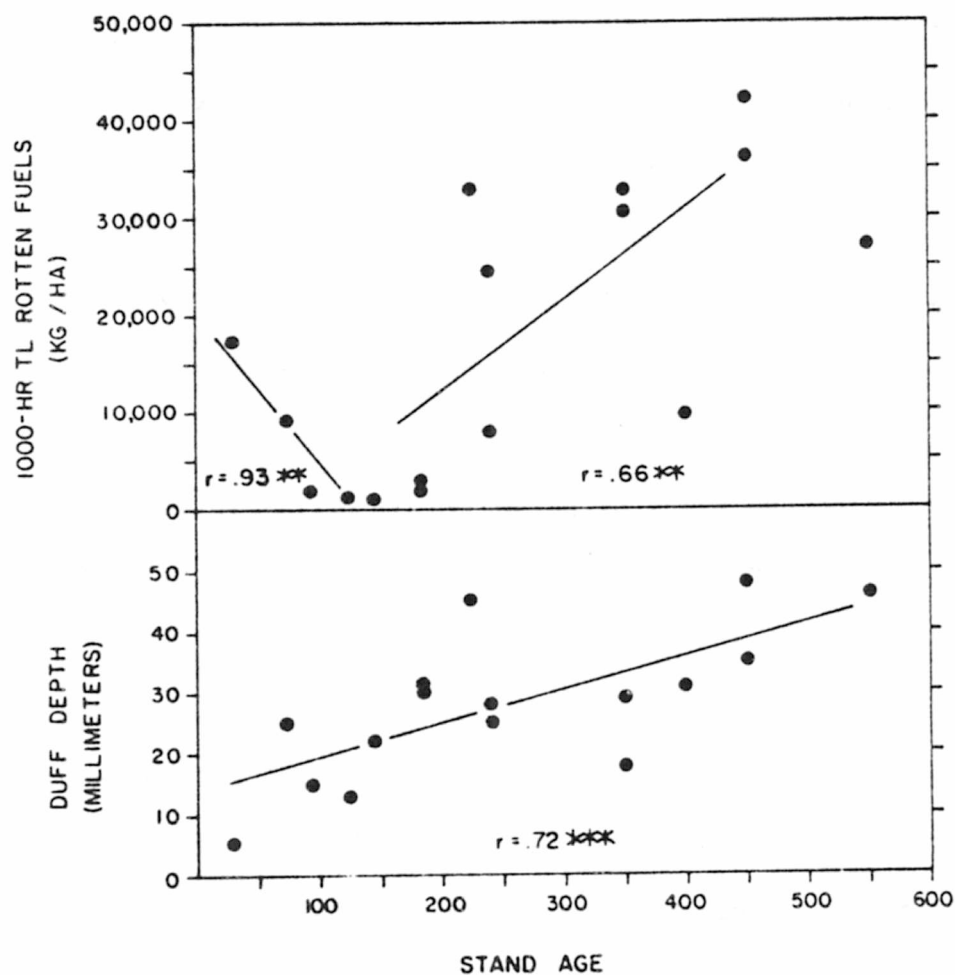


Figure 5. Changes in fuels in which a fire may persist during periods of unfavorable weather along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (** = 95% significance level; *** = 99%).

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 Figures 2-5, sample variance (s^2) in 20 transects increased significantly (>90% confidence level) with stand age for 1-HR TL fuels, needle litter depth, 1000-HR TL rotten fuels, and duff depth (Table 2-3, App. 2). This supports Despain and Sellers' (1977) qualitative observation that the fine fuels supporting ignition and initial spread, as well as the fuels that allow a fire to persist during unfavorable weather, become distributed less homogeneously in older stands, resulting in local patches where the fuel accumulation is unusually high, interspersed with areas having relatively sparse fuels. These high-fuel patches probably are important for generating sufficient heat to ignite tree crowns and larger dead fuels as well as sustaining smoldering fires (Despain and Sellers 1977).

Needle litter depth appears to be negatively correlated with site index in stands 200-600 yr old (significance level 97.5%, $r = -.77$ (Table 2-1, App. 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 that I used may be in error. Otherwise I found no correlations (significance level >90%) between site index and fuel accumulation.

Long-Term Patterns in Landscape Diversity

For a simulation of long-term patterns in landscape diversity, it was first necessary to choose a starting point. One possibility would be to begin at the present, or in the mid-1900's when fire control first became effective, then to project the vegetation mosaic into the future. Forecasting the changes that would occur during the next 200 yr with a policy of total fire exclusion is relatively easy based on current rates and patterns of forest succession. However, it is very difficult to predict with any certainty when and where fires would burn under a natural fire regime. Fire would be likely in nearly all late-successional stands, but the actual time of occurrence would be stochastic, ranging over decades or centuries.

Therefore, I chose instead to begin in 1778 and determine how today's landscape might differ if 20th-century man had entered the Yellowstone region 200 yr earlier. This approach was possible because I was able to reconstruct the vegetation mosaic existing at that time on the Little Firehole River Watershed based on the present age of forest stands (Fig. 6). 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 1778-1978 there were 4 major fires under the natural fire regime; 0 under total fire exclusion; and 3 under selective fire control, a very large fire in 1795 being

eliminated.

I first examined changes in the proportion of the Watershed covered by early, middle, and late successional stages under the three scenarios, combining the Pico/Cage and Abia/Vasc habitat-types for this analysis. Early stages include the period of tree re-establishment immediately following a destructive fire (community-types 1 and 2, Table 1; stand age 0 - ca 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 ca 40 - ca 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 ca 250+ yr). Meadows, riparian forests, and steep-slope forests, which together cover 16% of the watershed, were assumed to have remained constant.

Figure 7 shows a 240-yr simulation of landscape changes under three different fire regimes, the hypothetical selective fire control and total fire exclusion policies being in effect from 1778-1978. Points for the years prior to 1778 are estimates based on the size of major fires in 1739 and 1755, which apparently occurred after a long, relatively fire-free period (Fig. 1). In 1738 the watershed was dominated by late successional forests, with only small areas covered by early and middle stages. Extensive fires in 1739 and 1755 sharply reduced the old-growth forest and created a large area of early successional stages. Under the

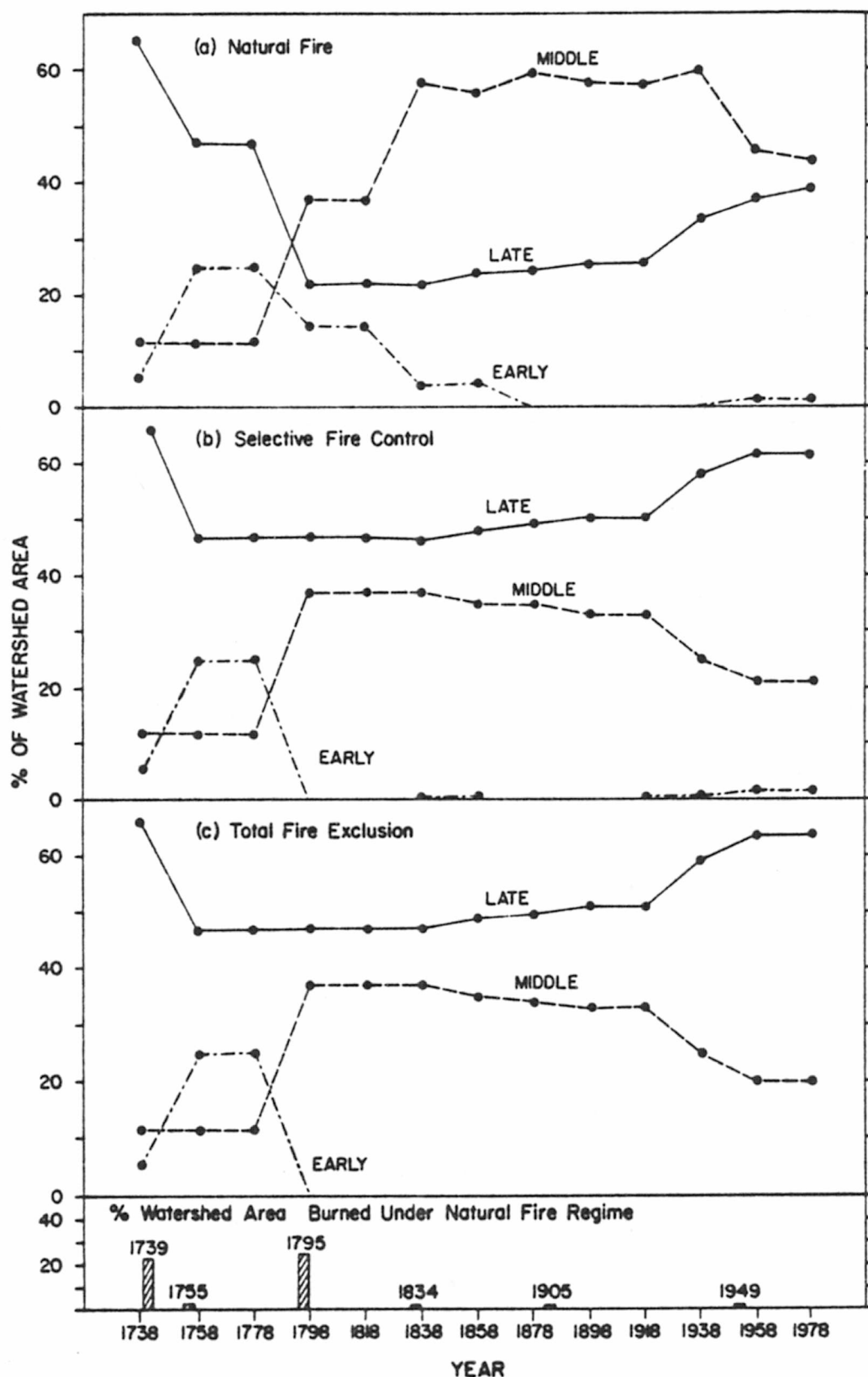


Figure 7. Percent of area on the Little Firehole River Watershed covered by early, middle, and late forest successional stages since 1738 under three different simulated fire regimes: (a) natural fire; (b) selective fire control; and (c) total fire exclusion (see text).

natural fire regime (Fig. 7a) the late successional stages were further reduced in 1795, with creation of another large area of early successional stages. By this time the areas burned in 1739 and 1755 had progressed into the middle successional stages; thus early, middle, and late successional forests were all well-represented in the landscape of 1798. After 1800 the area covered by early successional stages declined steadily and has remained very low (<5%) since the mid 1800's, reflecting the lack of large fires during the last 180 yr. In contrast, the amount of area covered by middle successional stages increased dramatically after 1798 and remains the most abundant type on the watershed today, a result of forest development on the areas burned in 1739 and 1795. 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. 7b), 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. 7c) shows patterns similar to selective fire control except that early

successional stages are absent after 1800.

Figure 8 shows changes in the area covered by early, middle, and late successional stages in the Pico/Cage and Abia/Vasc habitat-types under a natural fire regime. Major patterns are similar in the two habitat-types except that changes in the Abia/Vasc habitat-type occur 40-50 yr earlier than corresponding changes in the Pico/Cage habitat-type. This is because the large fire in 1739 burned primarily in the Abia/Vasc habitat-type, whereas in 1795 mainly the Pico/Cage habitat-type was affected. These two large fires each produced a dramatic but relatively short-lived increase in the area covered by early successional stages, followed by a prolonged increase in middle successional stages.

Figure 9 shows long-term patterns in landscape diversity indices based on ten community-types (Table 1). Changes in the richness index (Fig. 9a) reflect primarily the appearance and disappearance of two short-lived early successional stages that follow major fires (community-types 1 and 2). In 1778 only nine community-types were present, the early herbaceous stage (community-type 1) having disappeared since the last major fire in 1755. Under a natural fire regime the large fire in 1795 re-introduced this stage, but by then the seedling-sapling stage (community-type 2) had disappeared from areas burned earlier and in 1798 there were again only nine different community-types present. Succession appears to have occurred more slowly than usual on some areas burned in

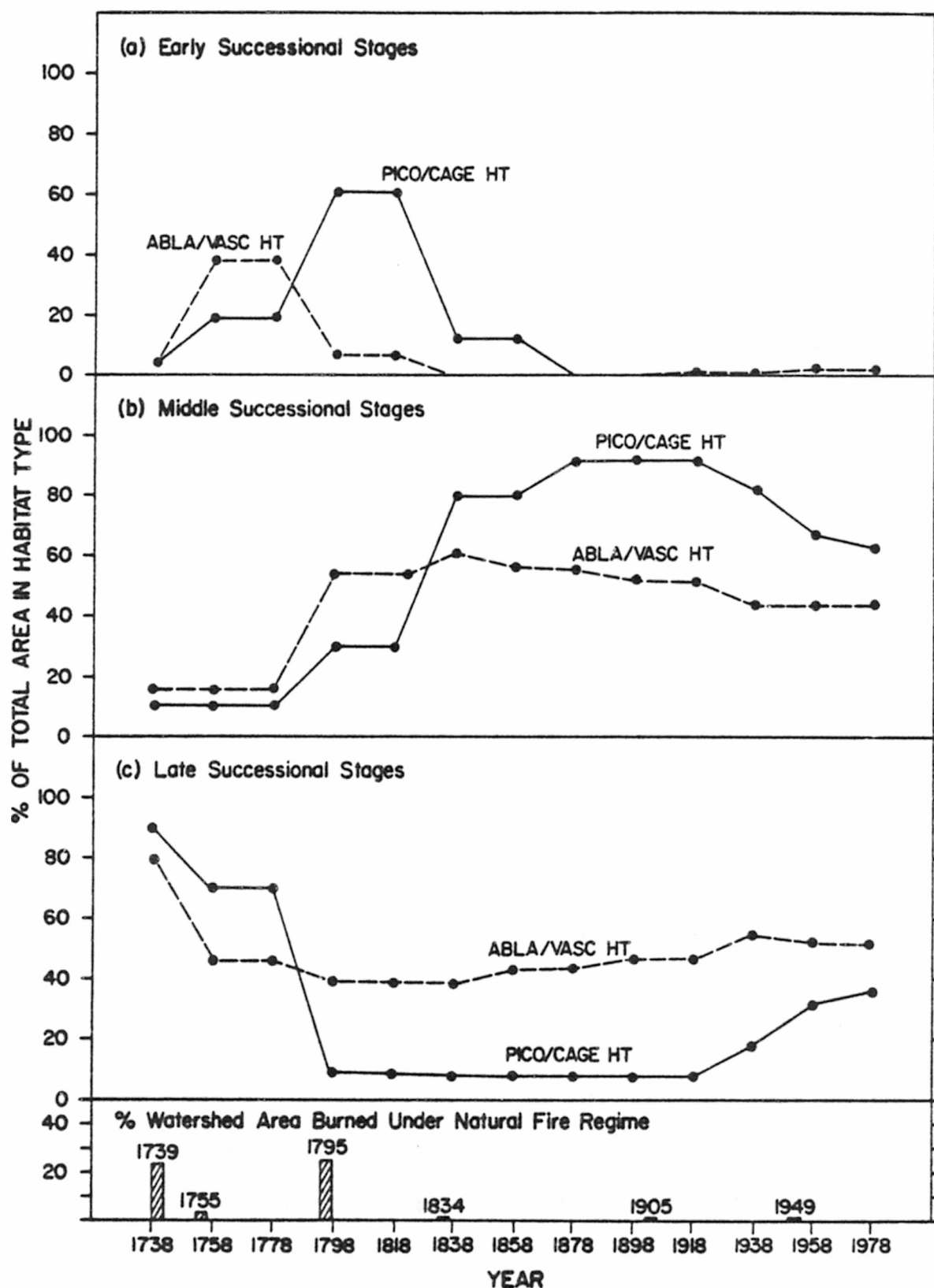


Figure 8. Percent of area in the Pico/Cage and Abia/Vasc habitat-types (HT) covered by early, middle, and late forest successional stages since 1738 under a natural fire regime.

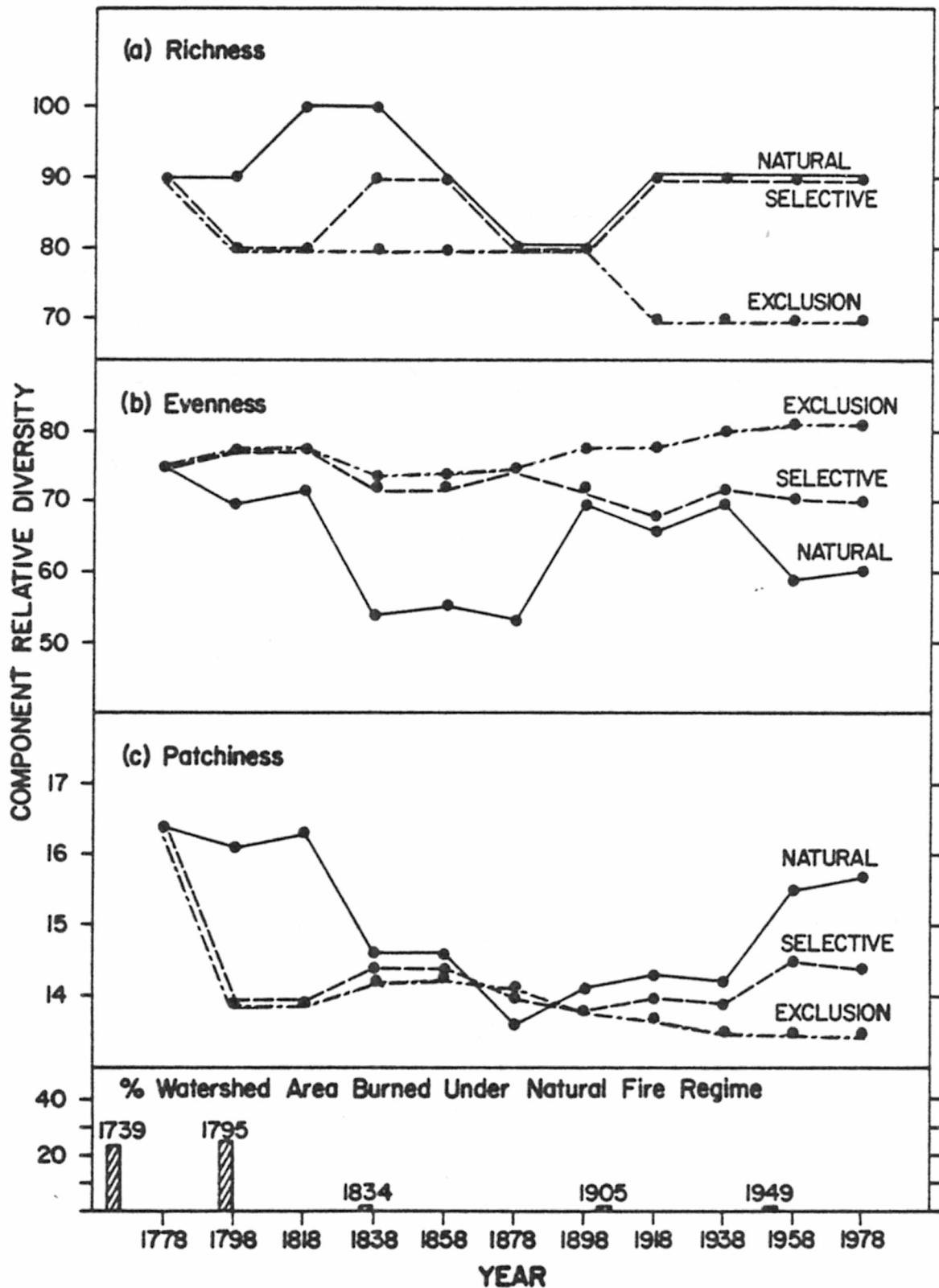


Figure 9. Relative richness, relative evenness, and relative patchiness on the Little Firehole River Watershed since 1778 under three different simulated fire regimes: natural fire — all fires allowed to burn; selective fire control — large fires excluded, small fires allowed to burn; total fire exclusion (see text).

1795, with prolongation of the two early stages (as described in Study Area section). Succession occurred normally over most of the area, however, and all ten community-types were present on the Watershed during the early 1800's. Richness declined thereafter, reaching 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. Major fires in 1905 and 1949 have increased richness during the 20th century, but because of the long intervals between fires, all ten community-types have not been present simultaneously again since the early 1800's. Had the 1795 fire been excluded under a selective fire control policy (Fig. 9a), the two early successional stages would have disappeared by 1800 and 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 early successional stages and eventually also the first middle successional stage (community-type 3) disappeared from the Watershed (Fig. 9a).

Long-term patterns in landscape evenness (Fig. 9b) can be interpreted by examining changes in the proportion of the Watershed covered by each of seven community-types representing upland forest successional stages (Fig. 10). The areas covered by three

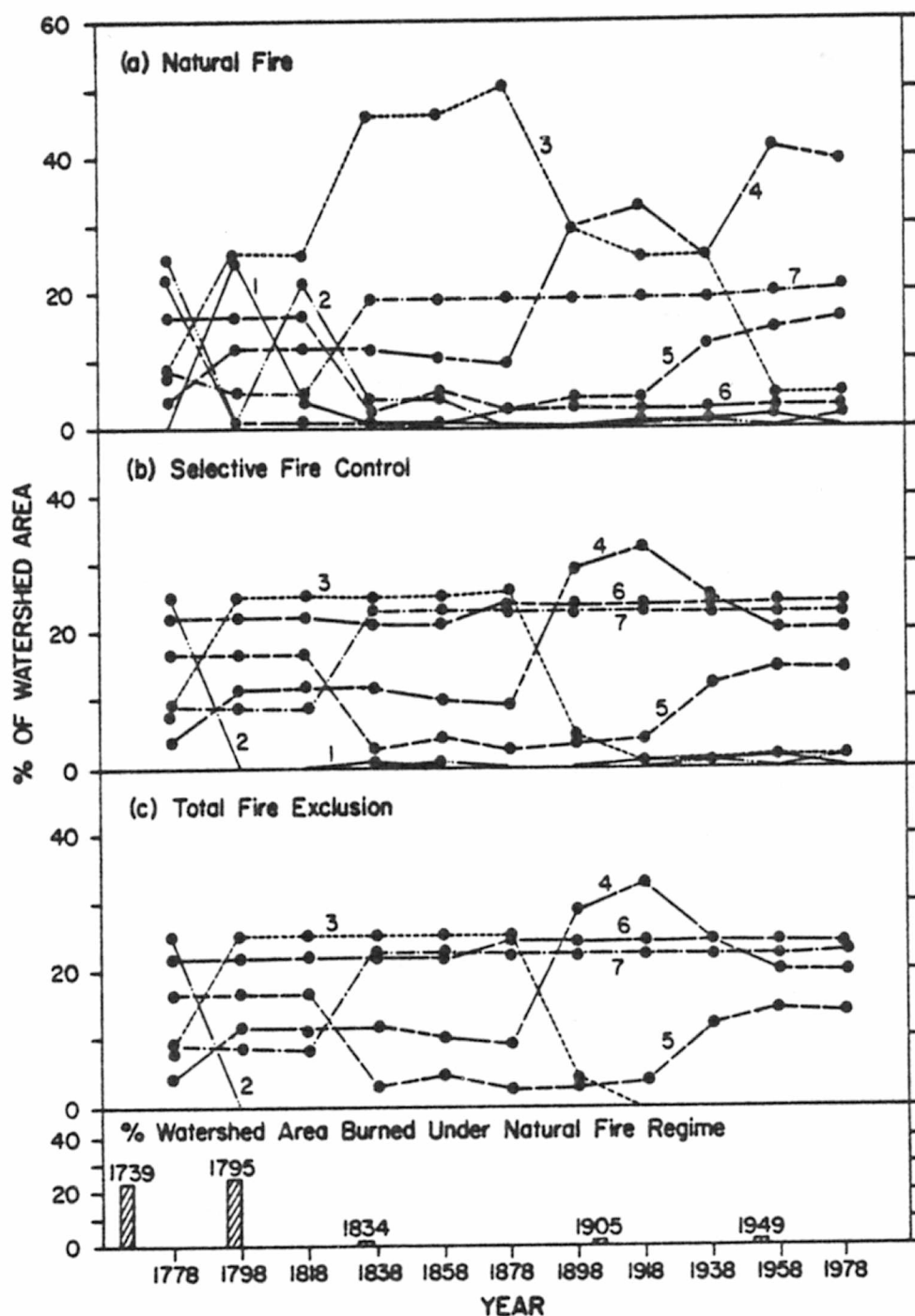


Figure 10. Percent of area on the Little Firehole River Watershed covered by each of seven upland forest successional stages since 1778 under three different simulated fire regimes: (a) natural fire -- all fires allowed to burn; (b) selective fire control -- large fires excluded, small fires allowed to burn; (c) total fire exclusion (see text). Forest successional stages (community-types) are defined in Table 1 and described in the section on Study Area.

other community-types (riparian forest, steep slope forest, and meadow), totalling 16% of the Watershed, were assumed to have remained constant and are not shown in Figure 10. Evenness under a natural fire regime declined sharply between 1818-1838 and remained low until the end of the 19th-century (Fig. 9b). Following a period of greater evenness in the early 20th century, the index again dropped between 1938-1958 and remains relatively low today (Fig. 9b). The first major reduction in landscape evenness during the mid-1800's occurred because 40-50% of the Watershed then became covered by a single community-type, i.e. immature pine forests developing after the extensive fires of 1739 and 1795 (Fig. 10a). By 1900 the forests on most of the area burned in 1739 had progressed to the mature pine forest stage and the Watershed area was more evenly distributed among community-types (Fig. 10a). The recent drop in landscape evenness since 1938 has occurred because most of the forests developing after 1795 have now also reached the mature pine forest stage, resulting again in a preponderance of one community-type and a low evenness index value (Fig. 9a, 10a). 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 (Fig. 10b) and landscape evenness would have been greater (Fig. 9b). The highest evenness values would have occurred with total fire exclusion (Fig. 9b). 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; whereas without fire the landscape would have been more evenly divided among a smaller number of middle and late successional community-types (Fig. 10c).

Landscape patchiness under a natural fire regime was high in 1778, after fires in 1739 and 1755, and remained high during the early 1800's following the 1795 fire (Fig. 9c). 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 is also due to local variation in the rate of succession plus the effects of the mountain pine beetle and another unidentified natural mortality agent (see Study Area) in forests developing on areas burned in 1795 in the Pico/Cage habitat-type. These organisms are producing early, extensive mortality in the dominant, even-aged lodgepole pine canopy in many stands, causing these stands to enter the next successional stage (transitional stage, community-type 5, Table 1) sooner than would ordinarily occur. Meanwhile, less severely affected stands nearby remain in the mature pine forest stage (community-type 4), and other stands in which initial tree restocking was unusually slow are still in the immature pine forest stage (community-type 3). The result is an intricate mosaic of community-types over much

of the Pico/Cage habitat-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 1938-1958 (Fig. 9c). This small increase would be due to patches created by small fires in 1834, 1905, and 1949 plus the effects of the mountain pine beetle in a small portion of the Pico/Cage habitat-type that burned in 1739. With total fire exclusion, landscape patchiness would have continued to decline into the 20th-century.

Figure 11 shows long-term patterns in overall landscape diversity, expressed first as a weighted average of relative richness, evenness, and patchiness (Fig. 11a). The evenness index generally varied oppositely from the richness and patchiness indices in my simulations, landscapes with high richness and patchiness frequently having low evenness and vice versa (Fig. 9). Because evenness was always high under the total fire exclusion policy (Fig. 9b), due to the reduced number of community-types present, an overall diversity index computed by averaging all three component indices indicates that landscape diversity usually would have been as high with fire exclusion as with natural fire or selective fire control (Fig. 11a). This index also indicates that overall landscape diversity would have been much lower in the late 1800's under a natural fire regime than under total fire exclusion (Fig. 11a), results which seem counter-intuitive. Therefore, I concluded that

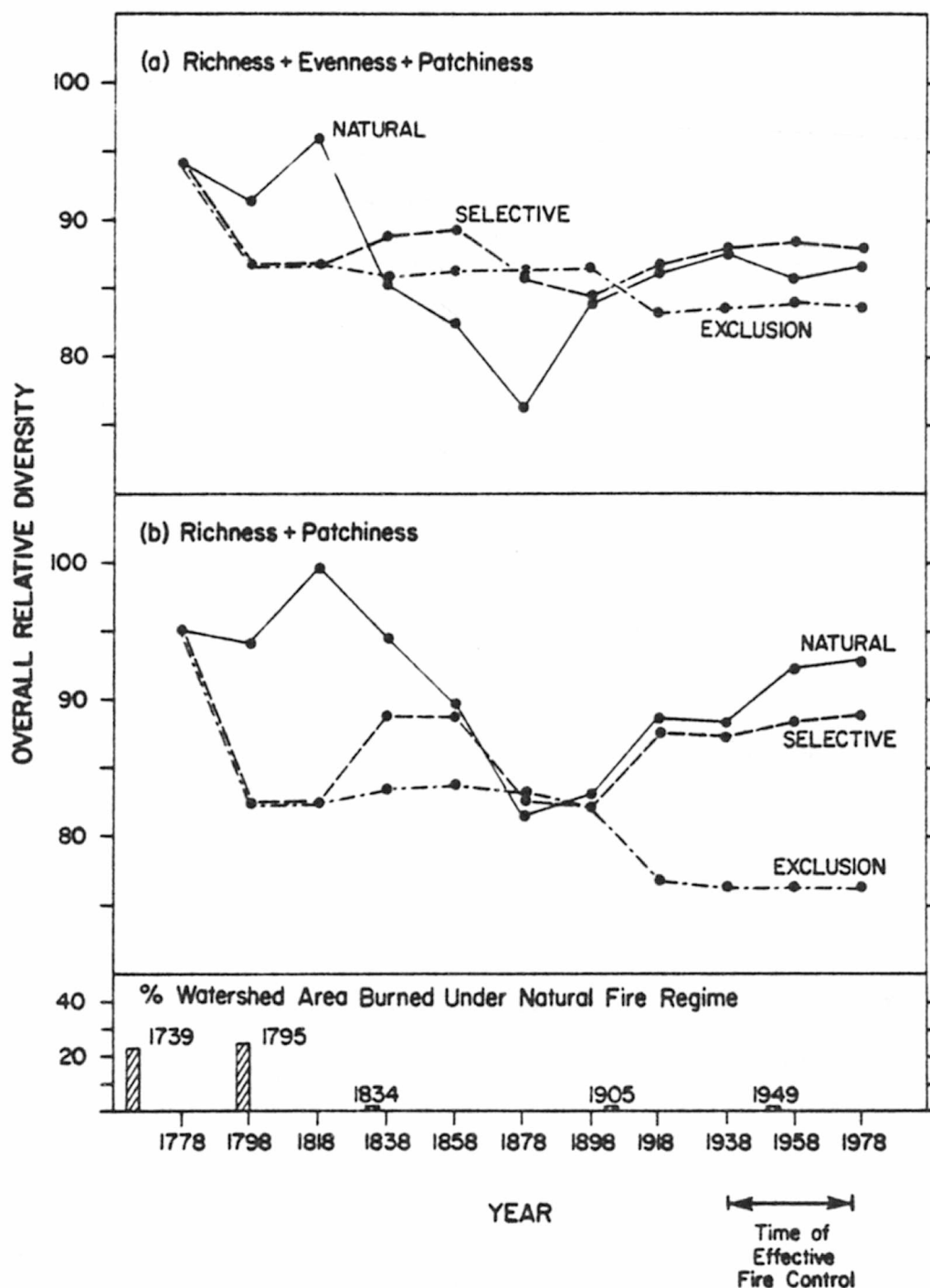


Figure 11. Overall landscape diversity on the Little Firehole River Watershed since 1778, expressed as: (a) a weighted average of the relative richness, relative evenness, and relative patchiness indices; and (b) a weighted average of the relative richness and relative patchiness indices (see text).

the evenness index provides a very different kind of information than the richness and patchiness indices, and it is inappropriate to combine the three by simple averaging. A weighted average of the richness and patchiness indices gives results that appear more meaningful (Fig. 11b). Using this index, overall landscape diversity under a natural fire regime was highest in the early 1800's following the large 1795 fire, falling to a low point in the late 1800's during a long period without major fires, then rising again in the 20th-century as two small fires and the pine bark beetle increased landscape richness and patchiness. Overall diversity would have been much less in the early 1800's under the selective fire control or total fire exclusion policies, but would have been equal under all three fire regimes during the low diversity period in the late 19th-century (Fig. 11b). Landscape diversity would have continued to decline during the 20th-century under total fire exclusion, whereas with selective fire control diversity would have increased after 1900, but not as much as occurred naturally (Fig. 11b). Note that overall landscape diversity on the Little Firehole River Watershed, expressed as a weighted average of richness and patchiness, has increased during the last 40 yr despite the fact that a fire suppression policy was in effect in Yellowstone National Park during most of this time (Fig. 11b).

DISCUSSION

Fire Cycles in Subalpine Forests of Yellowstone National Park

The fuels data in Figures 2-5 support Despain and Sellers' (1977) hypothesis that fire frequency in this area is controlled by the slow development during succession of a fuel complex capable of supporting an intense crown fire. Less intense surface fires do occur, but because even the maximum accumulations of fine fuels are comparatively low (Fig. 2) and because the small needles tend to form a relatively 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 the crown fires which may burn very large areas and produce major vegetational changes.

The very small quantity of easily ignited fine fuels in early successional stages (Fig. 2) makes a second fire unlikely during the first several decades following a destructive crown fire. A fire starting somewhere else may occasionally move into a recently burned area where it is supported by scattered rotten logs and herbaceous live fuels, as occurred in an uncontrolled fire that I observed in the Park in 1979. However, this fire was of extremely low intensity, being easy to walk through without discomfort.

This is quite a different situation from many other areas where very intense fires may develop in the fuels created by a recent fire on the same site (Brown and Davis 1973).

By stand age 150-200 yr fine fuels have accumulated to maximum levels (Fig. 2). However, at this time total fuel mass (Fig. 3) and canopy continuity (Fig. 4) are at very low levels. This means that a surface fire is unlikely to generate sufficient heat energy to ignite the tree crowns, and will therefore be restricted to the ground where it may burn through the fine fuels for a short distance but will probably go out before it covers a large area. This prediction is supported by observations of recent uncontrolled fires in Yellowstone National Park. A very intense crown fire burning rapidly through an old-growth spruce-fir forest stopped when it reached a 100-yr-old lodgepole pine forest, despite the fact that wind, temperature, and humidity all remained favorable and the pine forest was showered with fire brands (Despain and Sellers 1977).

Total fuel mass and canopy continuity reach high levels around stand age 250-300 yr and 350-400 yr, respectively (Figs. 3, 4). Fine fuels remain high (Fig. 2), having by this time become more heterogeneously distributed with locally large accumulations, and fuels in which fire can persist during unfavorable weather also have reached near maximum levels (Fig. 5). It can be seen, therefore,

that all of the fuel conditions necessary for an intense crown fire are not present simultaneously until after stand age ca 300-400 yr (Figs. 2-5). Small areas may burn in younger stands, but fires covering a large area and producing major vegetational changes are likely to occur only in old-age forests. Once the fuel complex has developed, the actual occurrence of a major fire is probabilistic, depending on when an ignition source and hot, dry, windy weather occur simultaneously (Sellers and Despain 1976, Despain and Sellers 1977). Therefore, I concluded that the average fire frequency or interval between successive destructive fires on a single site in subalpine forests of Yellowstone National Park must be a minimum of 300-400 yr, though it may be longer.

One additional piece of evidence indicating that fires in the past recurred at very long intervals is the fact that most lodgepole pine cones in this area are non-serotinous. In an environment characterized by frequent fire, selection would be expected to favor closed cones; whereas where fire-free intervals are often long enough to allow establishment of more than one pine generation between fires, open cones would be favored (Brown 1975). The latter condition appears to apply to subalpine forests in Yellowstone National Park.

Although I found evidence of a total of seven major fires plus eight very small fires during the last 350 yr, the vegetational composition of the Little Firehole River Watershed since 1800 has been dominated by the effects of two very large fires in 1739 and 1795 which together burned almost half of the 73-km² study area plus an undetermined amount of area adjacent to the Watershed. When the forest now developing on these areas again reaches the highly flammable late-successional stages 100-150 yr from now, another very extensive fire(s) can be expected. This leads to the hypothesis that coniferous forests on the subalpine plateaus of Yellowstone National Park, where topographic fire barriers are rare and site conditions relatively homogeneous, are characterized by a 300-400 yr fire cycle in which large areas burn during a short time period. Very large fires do not occur during the long intervening period because most of the landscape is covered by early and middle forest successional stages of relatively low flammability. The Little Firehole River Watershed presently is at a point about midway between major fire episodes in this cycle, which accounts for the low incidence and small size of fires during the last 150 yr (Fig. 1). Other subalpine watersheds in the Park may be in different phases of the cycle. Sellers and Despain (1976) suggested that fires larger than 4 km² are rare in Yellowstone National Park and that very few fires in the past exceeded 200 km². My results indicate that very large fires are

indeed infrequent, but that they do exert major, long-lasting effects on landscape patterns.

A 300-400-yr fire cycle may help to explain why the recent incidence of major fires since 1972 on the Two Ocean and Mirror Plateaus in eastern Yellowstone Park has been twice as great as the incidence during the last 350 yr on the Little Firehole River Watershed (Table 6). As noted above, the latter area appears to have been, since about 1800, in a phase where major fires are unlikely due to the vegetational composition of the landscape. On the much larger Two Ocean and Mirror Plateaus, however, there may be 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 incidence is that weather conditions conducive to a major fire have occurred more frequently during the last six yr than occurred on the average over the last 350 yr. This latter explanation seems unlikely however. Even if recent weather patterns may have been drier and warmer, fires could cover very large areas even during a single short period of favorable weather if a suitable fuel complex were 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 incidence and frequency. Clagg (1975) reported an average of 7.12 lightning fires per million acres per yr in

areas above 2575 m in Rocky Mountain National Park in northern Colorado, and estimated that 0.5 fires larger than 10 acres occurred per million acres per yr prior to 1870. Converting these data to metric units yields an incidence of 0.0018 fires/km²/yr for all fires and 0.00012 fires/km²/yr for major fires. The incidence of major fires appears to be substantially higher in Yellowstone National Park, with 0.00026 fires/km²/yr determined for the Little Firehole River Watershed and 0.00072 fires/km²/yr determined for the Two Ocean and Mirror Plateaus (Table 6). Total fire incidence also is higher on the Two Ocean and Mirror Plateaus, with 0.0031 fires/km²/yr (Table 6). I did not compare total fire incidence in my study area because, as noted earlier, the record of very small fires here is almost certainly incomplete. A comparatively lower fire incidence 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.

Arno (1976) reported very frequent fires in the past in sub-alpine forests of southern Montana, with mean fire-free intervals of 17-41 yr. This is quite different from my 300-400-yr estimate for fire frequency in Yellowstone National Park, a difference which apparently reflects a different interpretation of fire-scars. Arno searched for 50-200-ha areas in each vegetation-type containing at least 4-10 fire-scarred trees (preferably multi-scarred) and designated these areas as stands. He then divided the number of

years in the time period of interest by the total number of fires recorded in the stand to compute the average fire-free interval, assuming that (1) all the fires burned over the entire stand area, and (2) fire history in the stand is representative of the vegetation-type in general. I believe that both of these assumptions would be invalid in my study area. To illustrate, I located a 100-ha area in the Pico/Cage habitat-type containing fire scars from 1739, 1795, and 1834; for the period 1630-1978 this would give a mean fire-free interval of $348/3 = 116$ yr using Arno's interpretation. I believe this estimate is much too low for several reasons. First, groups of fire-scarred trees in this area appear to represent the margins of old burns. Although they may contain evidence of two or even three fires, each fire actually burned over a separate area except for small areas along the margins, an interpretation supported by the fact that the 100-ha area described above contains three different even-aged forests dating from 1739, 1795, and 1834. Thus, in my study area fire history in the immediate vicinity of fire-scarred trees appears not to be representative of the vegetation-type in general. Secondly, results of the fuels analysis (Fig. 2-5) and Rothermel's fire behavior model, using data from this area (App. 2), indicate that recurrent fires at intervals of only 100 yr are highly unlikely due to inadequate fuels. Finally, not all fire scars represent a major fire; in my study area I found several isolated fire scars caused by lightning or fire brands from a

fire some distance away with no evidence that the fire had burned more than several m^2 before extinguishing naturally. I believe it is important to distinguish between such very small local fires and the major fires which introduce large-scale vegetational change. The fire-scar interpretations recommended by Arno (1976) and Arno and Sneek (1977) are appropriate for ponderosa pine and other lower-elevation forests characterized by frequent, low-intensity fires; but I believe they seriously over-estimate fire frequency in lodgepole pine and spruce-fir forests at high elevations where fires tend to be infrequent and destructive. Arno's (1976) 17-41-yr estimate of the mean fire-free interval in the subalpine zone may more accurately reflect fire incidence over a large area rather than fire frequency on a single site.

Data on fuel accumulation in relation to stand age from other Rocky Mountain subalpine forests suggest that development of the fuel complex occurs more slowly in Yellowstone National 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 Figures 2-5 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 age 100-200 yr then declines steadily, in contrast to the pattern

in Yellowstone National Park (Figs. 2, 5) in which these components also reach high levels at 100-200 yr but then remain high or continue to increase. Clagg (1975) found that total dead woody fuels increased immediately after a fire, quickly declined to a low point at age ca 50 yr, then rapidly increased again to a peak at 100 yr, followed by a gradual decline until age ca 300 yr after which fuel mass appeared to remain constant. In contrast, Figure 3 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 (1975) also noted that fine fuels were 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

The diversity indices that I used in this study generally worked well for the measurement of landscape diversity even though some were originally developed for the measurement of species diversity in communities. The richness index was easy to compute and to interpret, although it is highly dependent on the particular classification system being used. Computation of the patchiness index was more complex, but it too provided results that appeared meaningful and interpretable. Patterns in landscape diversity as

measured with these two indices appear to have significance in relation to functional properties of the watershed system, as discussed below. The significance of patterns in the evenness index is less clear, however. Most ecologists tend to think of fire as a process that increases system diversity, but my results indicate that fire actually reduces the evenness component of landscape diversity. Whereas high evenness may enhance the overall diversity of species in a community, evenness may not have the same connotation at the landscape level.

A striking result of my 200-yr landscape reconstruction is that landscape composition and diversity on the Little Firehole River Watershed have fluctuated greatly under a natural fire regime (Figs. 7a, 9, 11). These results lead to the conclusion that the vegetation on this watershed has not been in a "steady-state" condition during the last 200 yr; and moreover, if the area is subject to a 300-400-yr fire cycle, as described earlier, then this particular landscape must be characterized over the very 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 one point in 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. The 73-km² Little Firehole River Watershed appears to represent a similar

stationary process of much greater size and complexity. One important difference here is that perturbation, rather than being random as Loucks indicated, is actually highly predictable due to changes in fire susceptibility during community development (cf Mutch 1970).

Loucks (1970) seems to imply that there may be some level of ecological organization at which a steady-state is achieved, i.e. where overall ecosystem structure and function remain relatively constant over time despite great fluctuations in individual component communities. Sprugel (1976), in a study of wave-regenerated fir forests in the northeastern United States, indicated that the entire fir forest ecosystem is in a steady-state condition despite wide-spread local patterns of community degradation and regeneration. 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 standing crop biomass on 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. There may be some level at which subalpine forests in Yellowstone National Park can be viewed as a steady-state system. However, if such a condition exists the area must be very large, certainly larger than a 73-km² 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 may be more appropriately viewed as a non-steady-state system characterized by cyclic, long-term changes in structure and function brought about by periodic large, destructive fires. Note that fire appears to control landscape dynamics not because it recurs very frequently, but because very large areas are affected when it does occur, and vegetational development between fires proceeds relatively slowly.

All evidence indicates that the normal stationary process on the Little Firehole River Watershed has 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 low fire-risk younger forests and topographically protected sites. 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, probably is well within the normal range of stochastic variation in fire frequency. It should be noted 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).

Concurrent with the changes in overall vegetational composition and landscape diversity shown in Figures 7 - 11, there must have been changes in functional characteristics of the Little Firehole River Watershed system. For example, with regard to hydrology, experiments in the southern Rocky Mountains have shown that total water yield increases >25% when forests are removed from 40% of a subalpine watershed, the effect lasting >20 yr and occurring primarily as increased spring run-off (Leaf 1975). Following the very large fires in 1739 and 1795, which together destroyed the forest on nearly 50% of the Little Firehole River Watershed, there probably was a significant increase in water discharge, which may have had an important effect downstream by cutting new stream channels and creating habitat for floodplain species such as willow and alder (cf Houston 1973). In addition, nutrient concentrations in stream-water often increase greatly for a short time after fire or deforestation (Likens et al. 1970, McColl and Grigal 1975), providing a periodic nutrient subsidy (*sensu* Odum et al. 1979) to aquatic ecosystems. Following this initial, brief nutrient pulse, Vitousek and Reiners (1975) have presented evidence that rapidly growing forests in early and middle successional stages assimilate nutrients

so efficiently that few remain available for leaching and stream-water concentrations are low; whereas in older forests where tree growth has slowed, relatively more nutrients are available for leaching and streamwater concentrations are higher. If this model is applicable to the subalpine ecosystem in Yellowstone National Park, the water from the Little Firehole River Watershed probably was nutrient-rich for a brief period immediately after the large fires in 1759 and 1795, but became relatively nutrient-poor as large portions of the Watershed were covered by rapidly growing young forests. As these pine forests have matured and tree growth has slowed during the last several decades, streamwater nutrient concentrations may have again increased. Long-term hydrologic and nutrient-cycling patterns such as these, though poorly understood at present, may have important bearing on the structure and productivity of aquatic ecosystems, including the large subalpine lakes in Yellowstone National Park in which total productivity and carrying capacity for fish appear to have declined during the last century (U. S. National Park Service 1975, Shero 1977).

Long-term patterns in landscape composition and diversity also have important implications for wildlife. The landscape of the early 1800's, with high richness and patchiness, probably provided high-quality habitat for a large number of animal species, including those adapted to the open environment of early successional stages (e.g. swallows, bluebirds, voles (Taylor 1969)) as well as those

favoring the closed forests of later successional stages (pine grosbeaks, grouse, squirrels (Taylor 1969)). During the period of low landscape diversity in the late 1800's, when early successional stages disappeared from the Watershed, the populations of animals requiring these habitats must have been greatly reduced, although some probably persisted in the meadows and sparsely-forested rocky areas. If we invoke the concept of a steady-state system for the Yellowstone subalpine ecosystem, as discussed earlier, then presumably the population declines in these early successional species on the Little Firehole River Watershed were balanced by population increases in other areas. However, if the Yellowstone ecosystem is instead a non-steady-state system, as hypothesized earlier, then populations of many animal species may periodically wax and wane in relation to the long-term fire cycle.

Habitat for elk (Cervus elaphus nelsoni V. Bailey) and other animals that utilize a variety of plant communities probably also has changed during the last 200 yr. Elk often are attracted to recently burned areas because of the greater production and nutritional quality of forage compared to surrounding forests (Davis 1977, Asherin 1973). The landscape of the early 1800's, containing a large newly burned area interspersed with patches of forest cover, probably afforded high-quality elk habitat (Thomas et al. 1976). Since the mid-1800's, however, with the development of dense, closed forests over most of the Watershed and the

associated reduction in herbaceous production (Taylor 1969), the attractiveness of this area to elk may have declined. Thus, it would appear that the quality of ungulate habitat on the high plateaus of Yellowstone National Park may be characterized by cyclic changes, with short periods of unusually high-quality habitat occurring every 300-400 yr followed by a longer period of somewhat less favorable habitat. Although such a cycle could have important implications for elk population dynamics in the Park, several other factors must also be considered. First, being very adaptable animals (Cole 1969, Houston 1976), the elk probably switch readily to other foods when the high-quality forage in recent burns begins to diminish due to re-forestation. Secondly, meadows and riparian forests also provide a large amount of forage for elk (Cole 1969); and in contrast to the unpredictable, short-lived openings created by fire, these areas remain a relatively constant landscape feature. The elk undoubtedly use recently burned areas whenever available, but the meadows and riparian forests probably have a greater long-term influence on elk distribution. Finally, it must be remembered that the subalpine zone constitutes primarily summer and fall habitat for elk. Such habitat in Yellowstone National Park is plentiful compared to the more restricted winter habitat, conditions on the winter range probably being a more important factor controlling elk population density (Houston 1976).

Figures 7 and 8 show that early forest successional stages are relatively transient features of the natural landscape in this area. The open habitat created by a fire usually lasts only 40 yr or less before being replaced by the closed forests of middle and late successional stages which then often remain for centuries until the next fire. Thus, except for the period immediately after the infrequent very large fires, only a small portion of the landscape consists of early successional stages, these frequently occurring as small patches or "islands" within an extensive closed forest. It is perhaps surprising then that Taylor (1969, 1973, 1974) found a larger number of plant and animal species associated with these early successional stages than with later forest stages. This poses interesting questions regarding colonization of these rare, unpredictable patches of favorable habitat as well as the population dynamics of the species involved. Studies on oceanic islands (MacArthur and Wilson 1967, Sullivan and Shaffer 1975) would suggest that small, isolated patches of early successional vegetation may be characterized by greater local extinction rates and a smaller number of species than larger patches located closer to a population source. These studies also would suggest that the early successional species must possess efficient dispersal mechanisms. However, although the island analogy is useful in this context, it should be applied with some caution because the habitats existing in early forest successional stages actually are not as

disjunct as oceanic islands. Small populations of early successional species probably survive between fires in meadows, rocky areas, and small forest glades; from these "refugia" they can quickly colonize the open habitat created by a nearby burn. Moreover, only a few of Taylors' (1969, 1973, 1974) early successional species were absolutely restricted to these habitats; most had the highest population densities in recently-burned areas, but low densities were also present in older forests (cf Lyon and Stickney 1976).

In addition to the changes in landscape composition and diversity attributable to fire and forest succession during the last 200 yr, there appears to have been a small increase in the total forested area on the Little Firehole River Watershed as forest margins have slowly advanced into meadows. Moist, alluvial meadows with very dense herbaceous growth have not been affected, but comparatively dry, upland meadows appear to be gradually disappearing from the landscape. A 1-ha area shown as a meadow on a topographic map prepared in 1956 is today filled by young lodgepole pine saplings 1-3 m tall. The area is recognizable as a former meadow by the presence of herbaceous species characteristic of open sites as well as the absence of recent fire scars (ruling out the possibility that it is a transient, fire-created opening). I found several small areas of 1 ha or less, particularly in the drier Pico/Cage habitat-type, containing these same meadow species and in which the trees were smaller and younger than in the surrounding forest.

This would indicate that many areas covered today by unbroken expanses of closed forest may have contained scattered small glades in the past, resulting in somewhat greater landscape diversity. I did not treat this pattern in my landscape simulations because of the very small size of these openings and the difficulty of determining exactly when forest encroachment may have begun. Moreover, changes in landscape composition and diversity attributable to forest advance during the last 200 yr are relatively minor compared to the striking patterns produced by fire.

The reason for this recent increase in forested area is not known, although it may be related to gradual climatic changes, the Yellowstone area apparently having become slightly warmer and perhaps drier during the last 200 yr (Houston 1976). I found no evidence that recent forest advance is related to fire suppression. Comparisons of today's landscapes with those shown in photographs from the late 1800's indicate that small increases in forest area and density have occurred in many subalpine areas within Yellowstone National Park and surrounding areas (Croft and Ellison 1960, Gruell 1973, Houston 1976). Patten (1963) also noted widespread forest advance in the Madison Range just northwest of the Park, interpreting it as an ongoing process of reforestation that has been taking place since the end of the xerothermic maximum period 4000 yr ago.

Management Implications

As discussed earlier, fire control efforts to date appear to have had a minimal impact on natural, long-term landscape patterns in the subalpine forests of Yellowstone National Park. However, it is clear from Figs. 7c, 9, and 11 that several decades or a century of effective, total fire exclusion could produce significant changes in some areas. Portions of the Park covered today by predominantly young and middle-aged forests, such as the Little Firehole River Watershed, might not be greatly affected by as much as a century of fire control because few fires would be likely during that time anyway. However, in areas where large fires have not occurred for 300-400 yr, a century of fire suppression could delay the onset of the next major fire cycle for an unnaturally long period; early successional stages would disappear and old-growth forests would dominate the landscape for an unusually long time (Fig. 7c). The current fire management plan (U. S. National Park Service 1975) 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 km², these being 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 no 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 parameters 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. 9 and 11). Using a carefully planned program of prescribed burning or timber harvesting it undoubtedly would be possible to maintain greater landscape diversity than occurs naturally. However, 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. 7 - 11 underscore the exhortations of Wright (1974), Sullivan and Shaffer (1975), 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.

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APPENDIX I

FIRE SCAR SAMPLE DATA

AND

FIRE MAPS

Table 1-1. Fire scar sample data. Explanations of column headings are as follows:

STAND: See Fig. 1-1 for stand locations.

SPECIES: Pico = Pinus contorta (lodgepole pine)

Pial = Pinus albicaulis (whitebark pine)

OUTER SCAR--RINGS: The number of annual rings counted from the cambium to the outermost fire-scar annulus. The superscript "a" indicates that tree growth was very rapid for many years after the scar was created.

DATE: The year in which the scar was created, determined by subtracting the number of annual rings between the scar annulus and the cambium from the year of sampling (1978).

INNER SCAR--RINGS: The number of annual rings between the outermost and innermost scar annulus (if present). Superscript "a" has the same meaning as above. Superscript "b" indicates that the rings were counted from the cambium to the innermost scar annulus because the outermost scar annulus was difficult to identify with certainty. The first sample tree in stand 57 contained three fire scars, the innermost one being reported on a second line beneath the middle fire scar.

RINGS TO PITH: The number of annual rings between the innermost fire scar and the pith.

HEIGHT FACTOR: The estimated age of the tree at the height of sectioning.

Table 1-1. (Continued)

TREE AGE: The estimated total age of the tree in 1978. The superscript "c" indicates that the tree grew rapidly during its early years.

Table 1-1. (Continued)				HEIGHT OF SECTION	OUTER SCAR		INNER SCAR		RINGS TO PITH	HEIGHT FACTOR	TREE AGE
STAND	DATE	SPECIES	DBH (cm)	(m)	RINGS	DATE	RINGS	DATE			
15	8-6-78	Pico	39	0.9	181 ^a	(1797)	56 ^a	(1741)	89	12	338 ^c
38	6-18-78	Pico	38	1.2	184 ^a	(1794)			40	9	233 ^c
40	6-19-78	Pico	33	1.2	180 ^a	(1798)			35	12	227 ^c
41	6-20-78	Pico	28	0.9	89	(1889)	97 ^a	(1792)	99	9	294 ^c
42	6-21-78	Pico	20	0.9	90	(1888)	92 ^a	(1796)	39	9	230 ^c
44	6-21-78	Pial	38	0.9	183 ^a	(1795)	152 ^a	(1643)	191	35	561
46	6-22-78	Pial	38	0.9	~240	(~1740)			250	35	~525
48	7-16-78	Pial	36	1.2	181 ^a	(1797)	53 ^a	(1744)	101	35	370
49	7-16-78	Pico	33	1.2	~179 ^a	(~1799)			32	12	223 ^c
51	7-17-78	Pico	22	1.7	183 ^a	(1795)			32	16	231 ^c
52	7-17-78	Pico	41	0.8	144 ^a	(1834)	36 ^a	(1798)	36	8	224 ^c
52	7-17-78	Pico	17	2.4	181 ^a	(1797)			26	24	231 ^c
53	7-17-78	Pico	24	1.8	183 ^a	(1795)			30	18	231 ^c
54	7-17-78	Pico	29	0.9	183 ^a	(1795)			30	9	222 ^c
55	7-18-78	Pico	20	0.9	~ 42	(~1936)	183 ^{ab}	(1795)	32	10	225 ^c

Table 1-1. (Continued)

STAND	DATE	SPECIES	DBH (cm)	HEIGHT OF SECTION (m)	OUTER SCAR RINGS	DATE	INNER SCAR RINGS	DATE	RINGS TO PITH	HEIGHT FACTOR	TREE AGE
56	7-18-78	Pial	38	1.2	183 ^a	(1795)	56 ^a	(1739)	277	50	566
57	7-20-78	Pico	41	2.4	~120	(~1858)	183 ^{ab}	(1795)	80	24	343 ^c
							56 ^a	(1739)			
57	7-20-78	Pico	25	1.2	~119 ^a	(~1859)	32 ^a	(~1827)	43	12	206 ^c
				1.5	181	(1797)			141	15	
58	7-22-78	Pico	23	0.6			54 ^a	(1743)	102	6	343 ^c
58	7-22-78	Pico	28	0.9	184 ^a	(1794)			147	9	340 ^c
59	7-23-78	Pico	24	0.9	~185 ^a	(~1793)	56 ^a	(~1737)	71	30	~342
62	7-24-78	Pico	32	1.2	181 ^a	(1797)			37	12	230 ^c
63	7-24-78	Pico	29	1.2	183 ^a	(1795)			45	12	240 ^c
64	7-24-78	Pico	28	1.2	181 ^a	(1797)	61 ^a	(1736)	92	12	346 ^c
65	8-6-78	Pico	32	1.2	~176 ^a	(~1802)			30+3	12	221 ^c
67	8-7-78	Pico	20	1.2	29 ^a	(1949)					
67	8-7-78	Pico	20	1.1	29 ^a	(1949)					
67	8-7-78	Pico	25	1.2	29 ^a	(1949)					

Table 1-1. (Continued)

STAND	DATE	SPECIES	DBH (cm)	HEIGHT OF SECTION (m)	OUTER SCAR RINGS	DATE	INNER SCAR RINGS	DATE	RINGS TO PITH	HEIGHT FACTOR	TREE AGE
68	8-7-78	Pico	28	1.2	~ 66 ^a	(~1912)			94	12	172 ^c
68	8-7-78	Pico	20	0.9	29 ^a	(1949)			30	10	69
69	8-7-78	Pico	23	0.9	29 ^a	(1949)			116	18	163
72	8-8-78	Pial	36	0.9	~127	(~1851)					
73	8-9-78	Pico	51	0.9	71	(1907)	152 ^a	(1755)	172	20	415
74	8-9-78	Pico	30	0.9	73 ^a	(1905)			74	10	157
76	8-13-78	Pico	34	1.2	~232 ^a	(~1746)			74	12	318 ^c
78	8-14-78	Pico	34	0.9	236 ^a	(1742)			92	9	337 ^c
79	8-14-78	Pico	36	0.9	235 ^a	(1743)			71	9	315 ^c
80	8-14-78	Pico	32	0.8	238- ^a 240	(1738- 1740)					
83	8-15-78	Pico	25	0.9	~ 97	(~1881)			101	20	~218 ^c
83	8-15-78	Pico	38	0.9	236	(1742)			76	9	321 ^c
84	8-15-78	Pico	27	0.9	237 ^a	(1741)			91	14	342
90	9-25-78	Pico	25	0.9	78	(1900)					

Table 1-1. (Continued)

STAND	DATE	SPECIES	DBH (cm)	HEIGHT OF SECTION (m)	OUTER SCAR RINGS	DATE	INNER SCAR RINGS	DATE	RINGS TO PITH	HEIGHT FACTOR	TREE AGE
90	9-25-78	Pico	20	0.9	~ 77 ^a	(~1901)					
94	9-24-78	Pial	46	0.6	239 ^a	(1739)	~ 80	(~1659)			

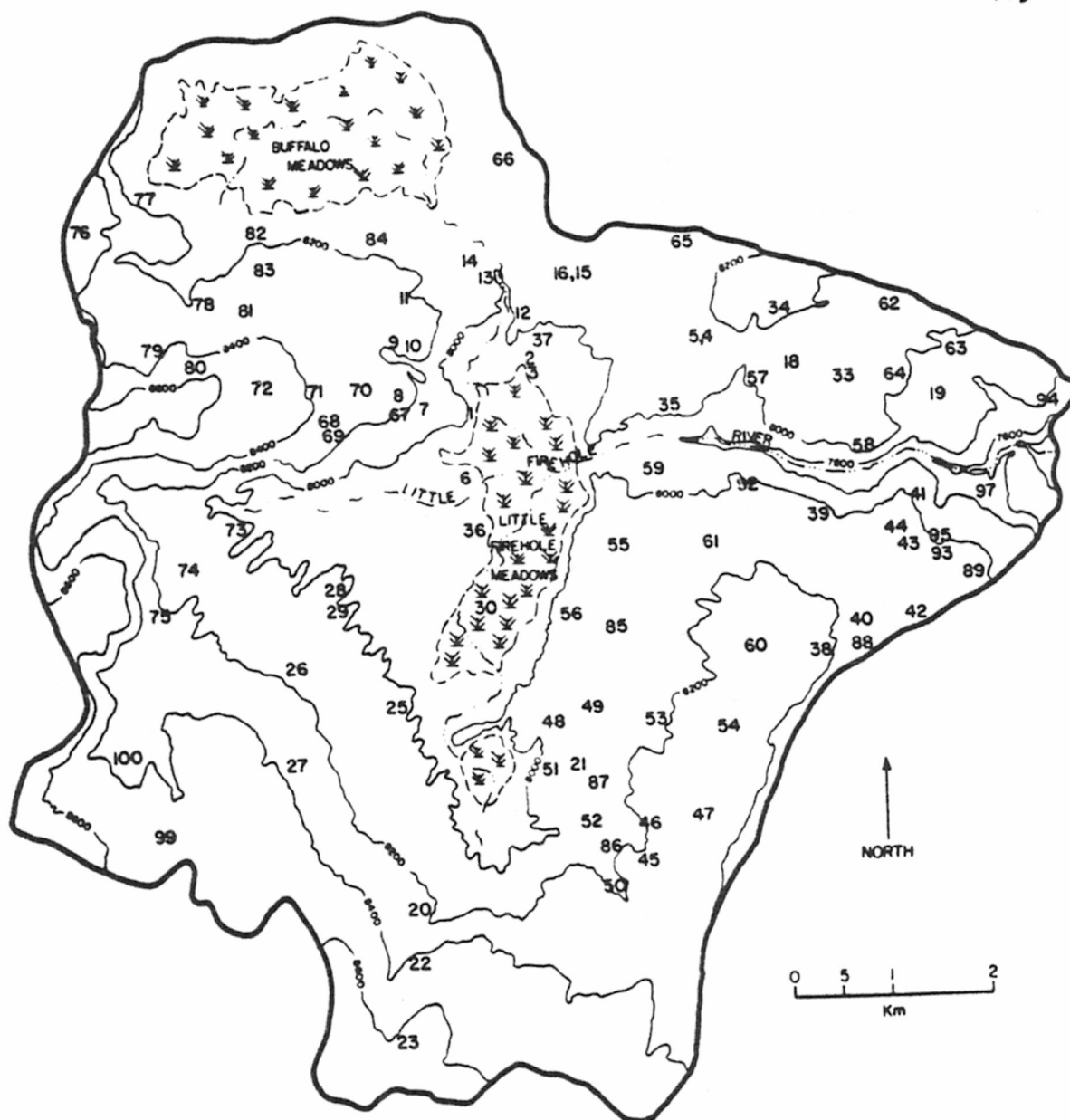


Figure 1-1. Location of sample stands (represented by numbers) on the Little Firehole River Watershed.

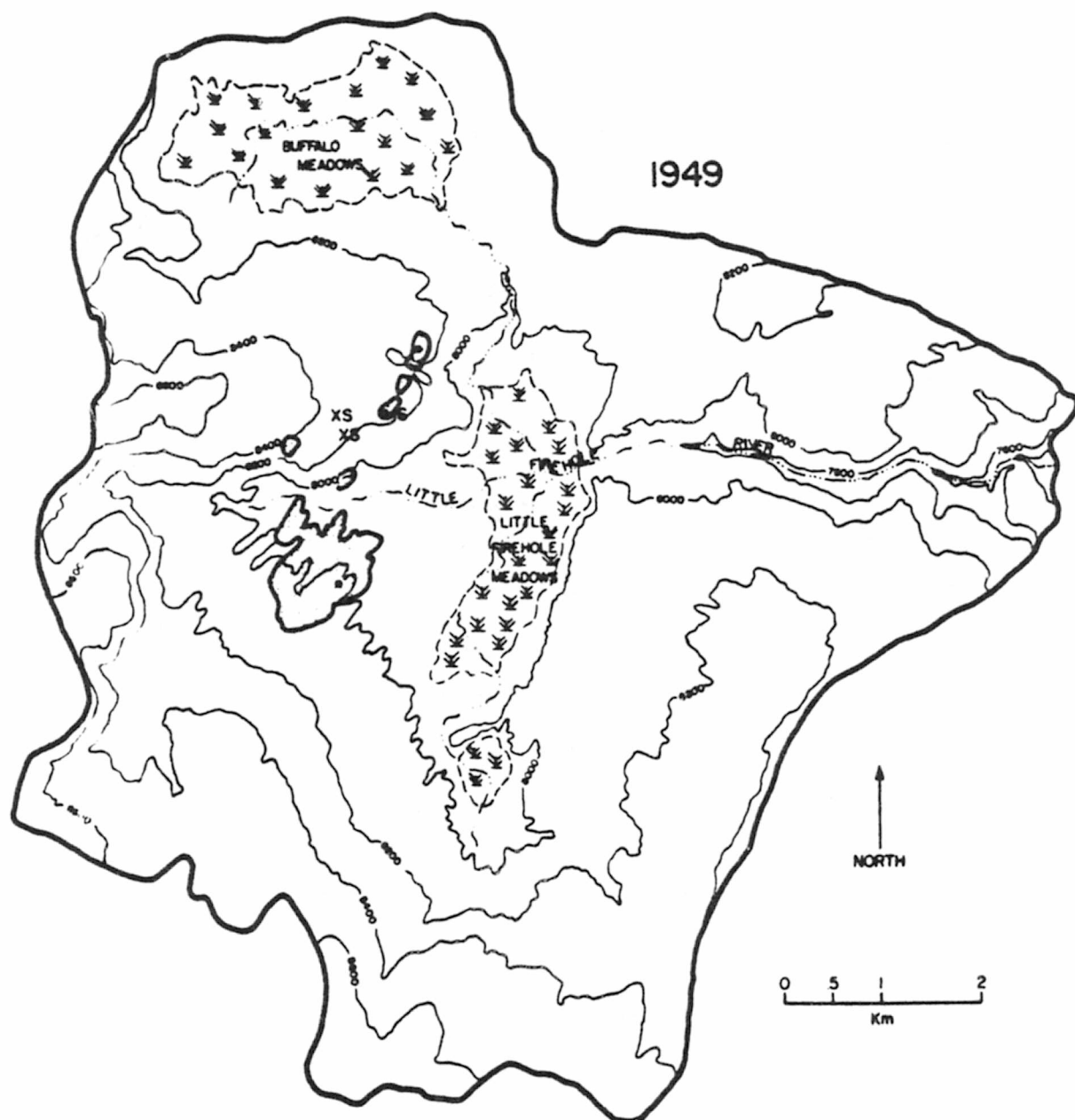


Figure 1-2. Areas burned by the major fire in 1949. ● S = fire scar plus even-aged lodgepole pine reproduction; XS = fire scar without even-aged pine reproduction; ○ = even-aged pine reproduction without fire scars.

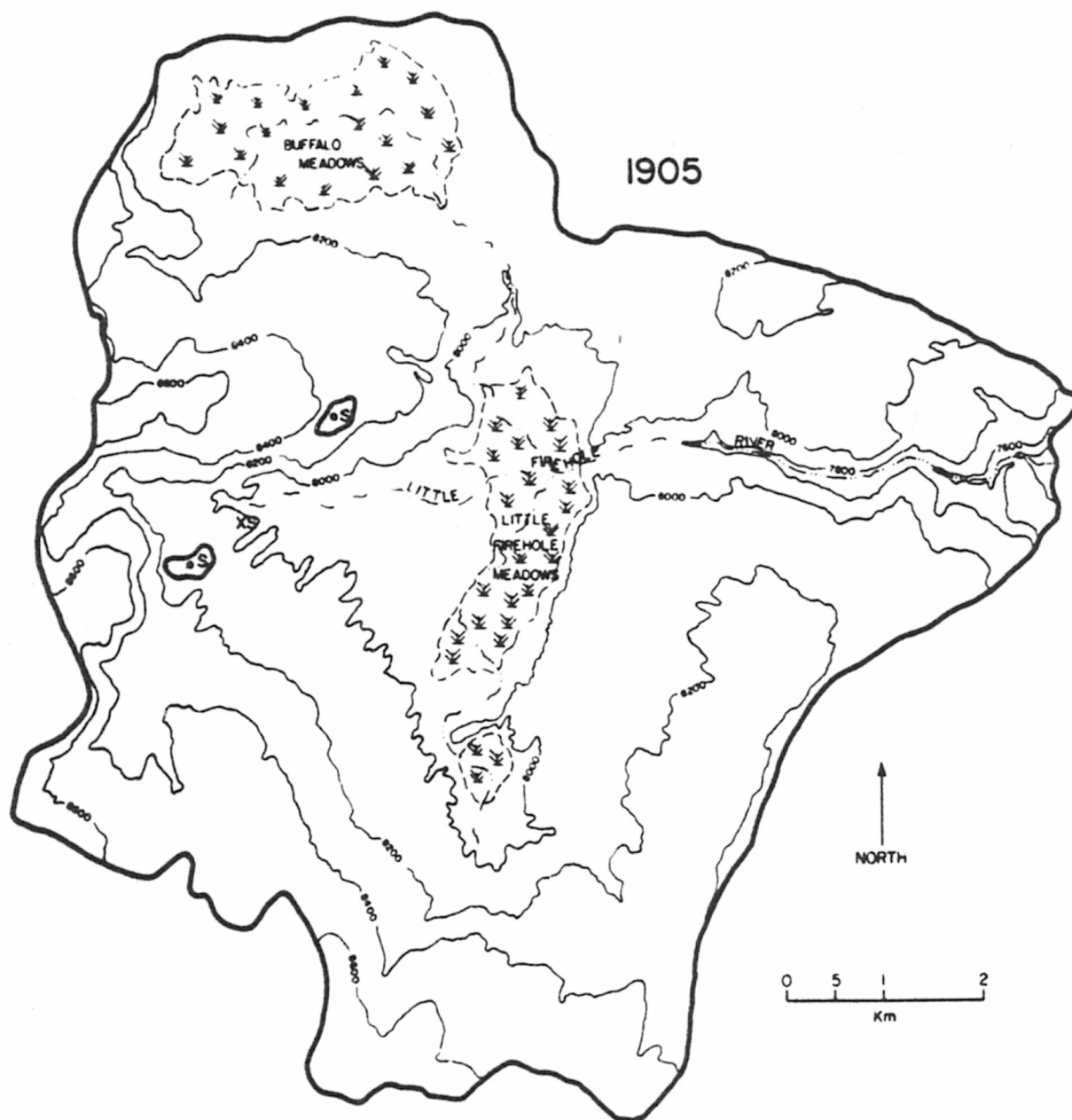


Figure 1-3. Areas burned by the major fire in 1905. ●S = fire scar plus even-aged lodgepole pine reproduction; XS = fire scar without even-aged pine reproduction.

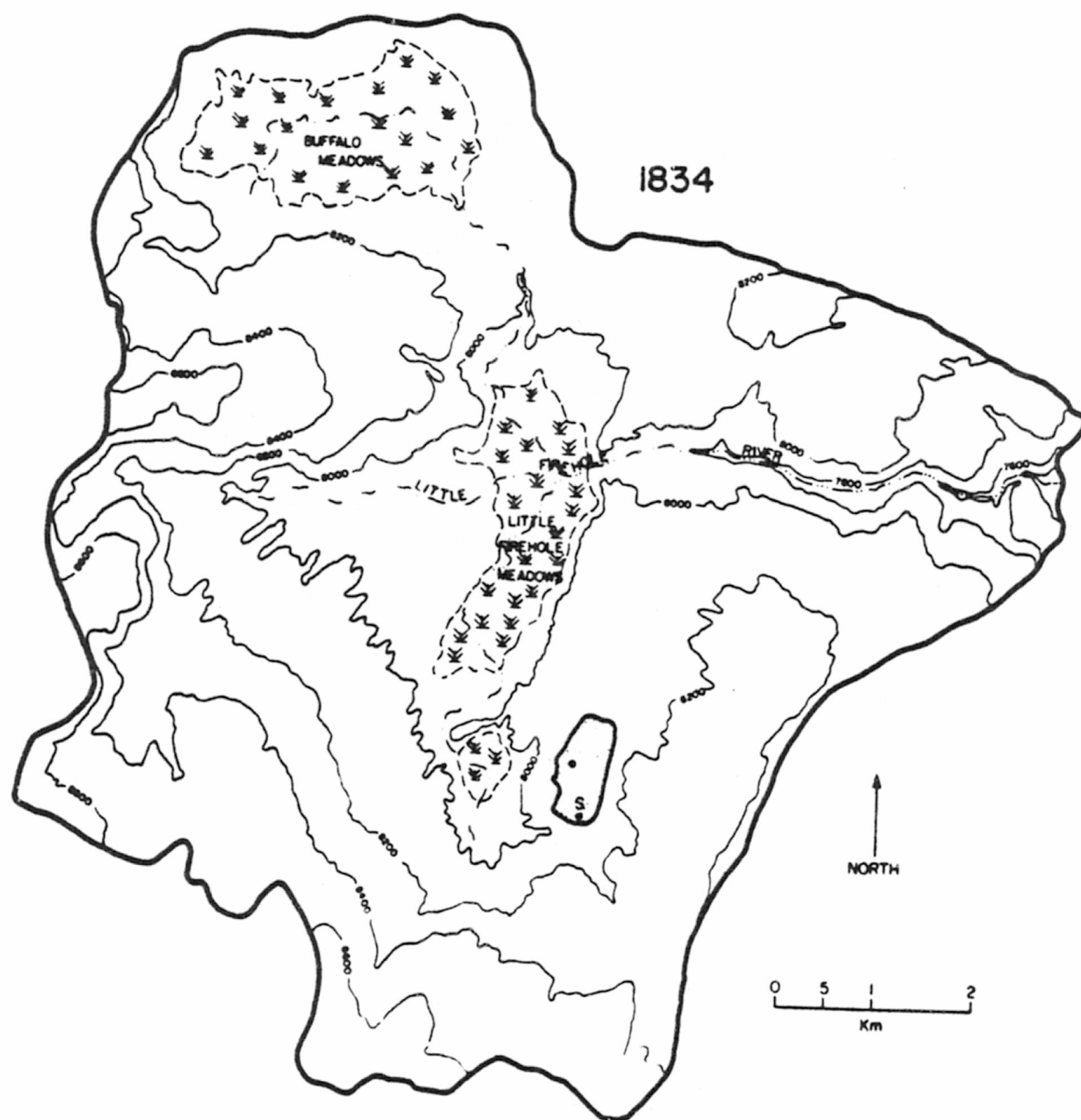


Figure 1-4. Areas burned by the major fire in 1834. ● S = fire scar plus even-aged lodgepole pine reproduction; ● = even-aged pine reproduction without fire scars.

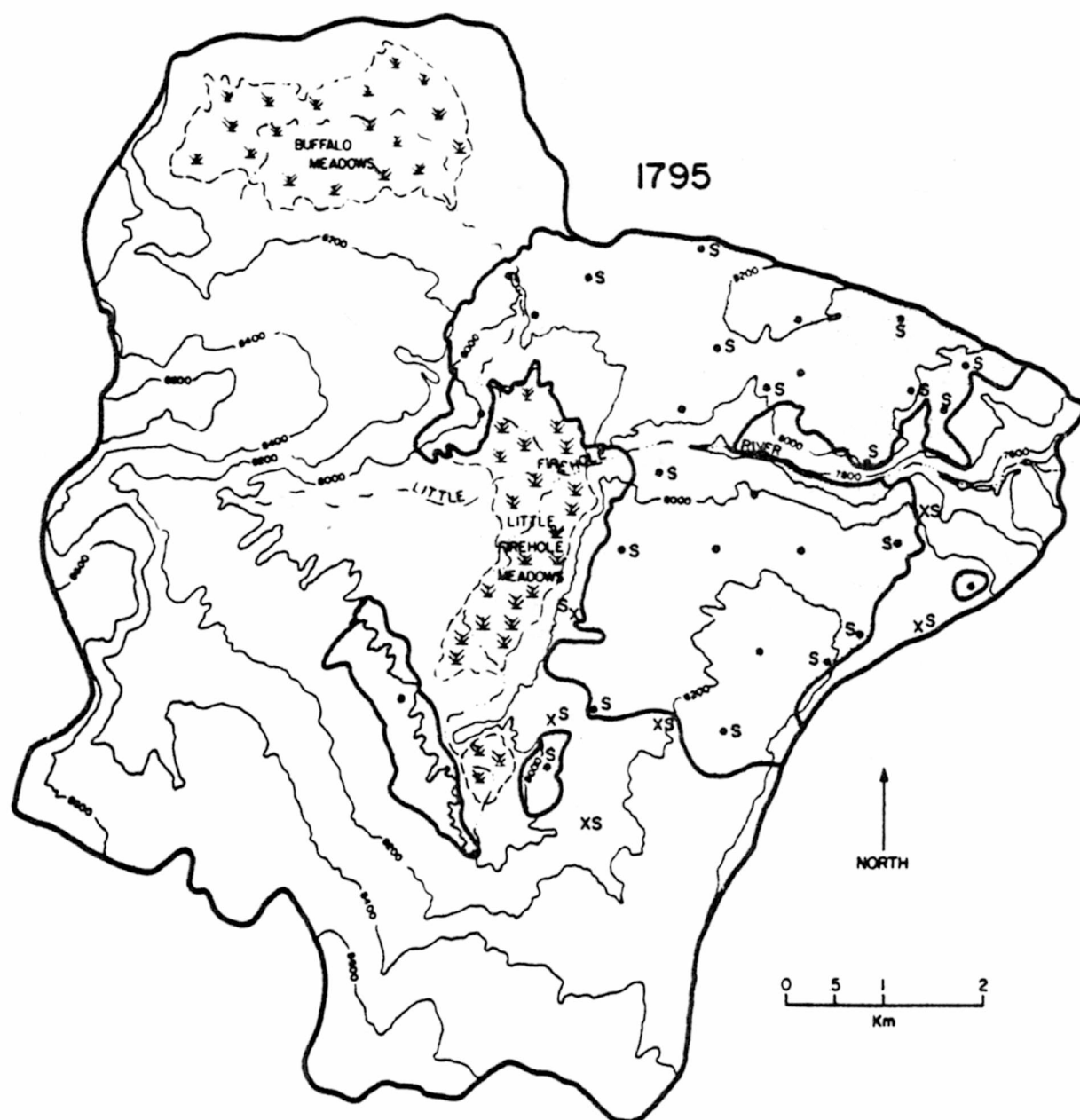


Figure 1-5. Areas burned by the major fire in 1795. ●S = fire scar plus even-aged lodgepole pine reproduction; XS = fire scar without even-aged pine reproduction; ● = even-aged pine reproduction without fire scars.

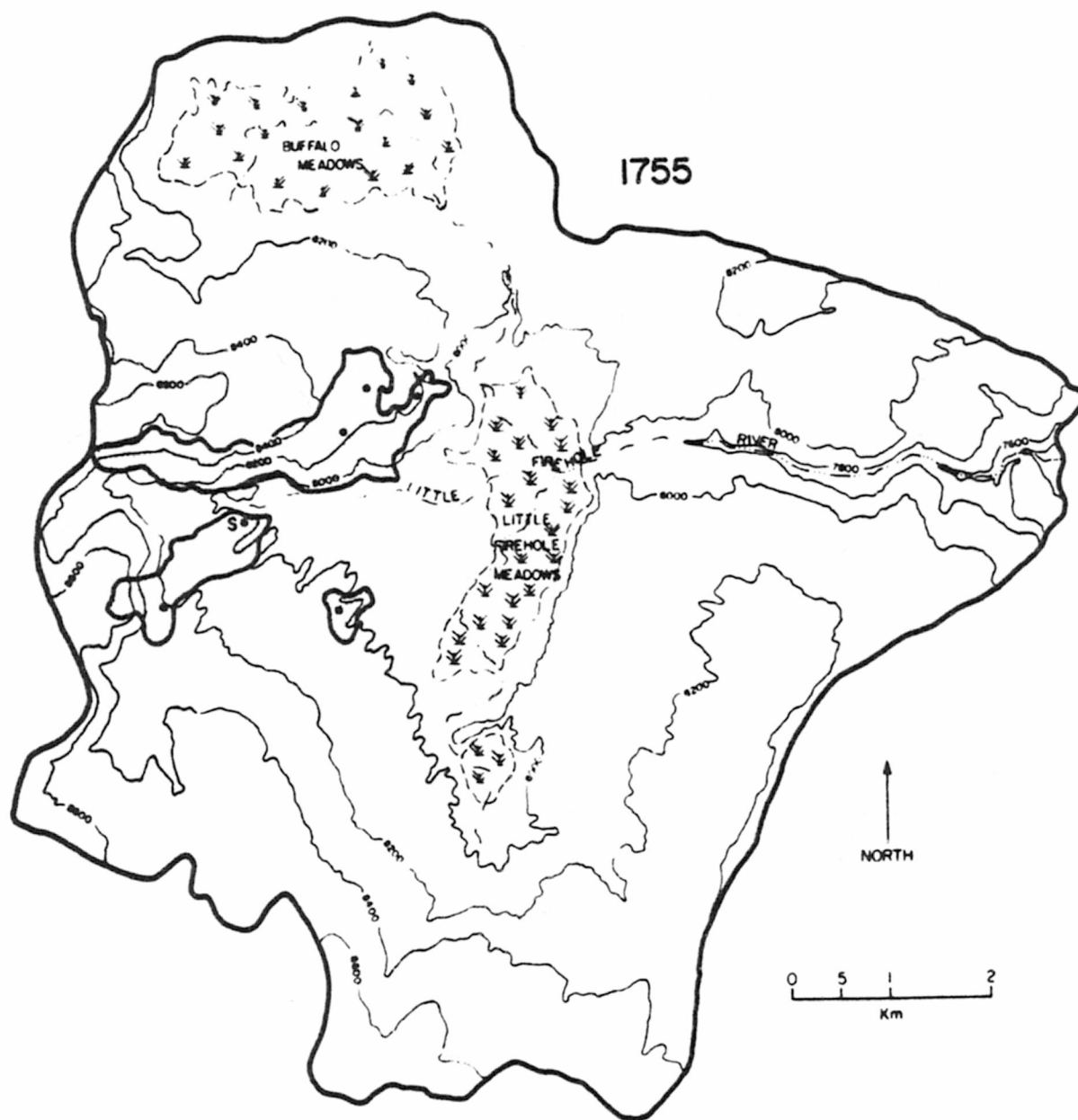


Figure 1-6. Areas burned by the major fire in 1755. ●S = fire scar plus even-aged lodgepole pine reproduction; ● = even-aged pine reproduction without fire scars.

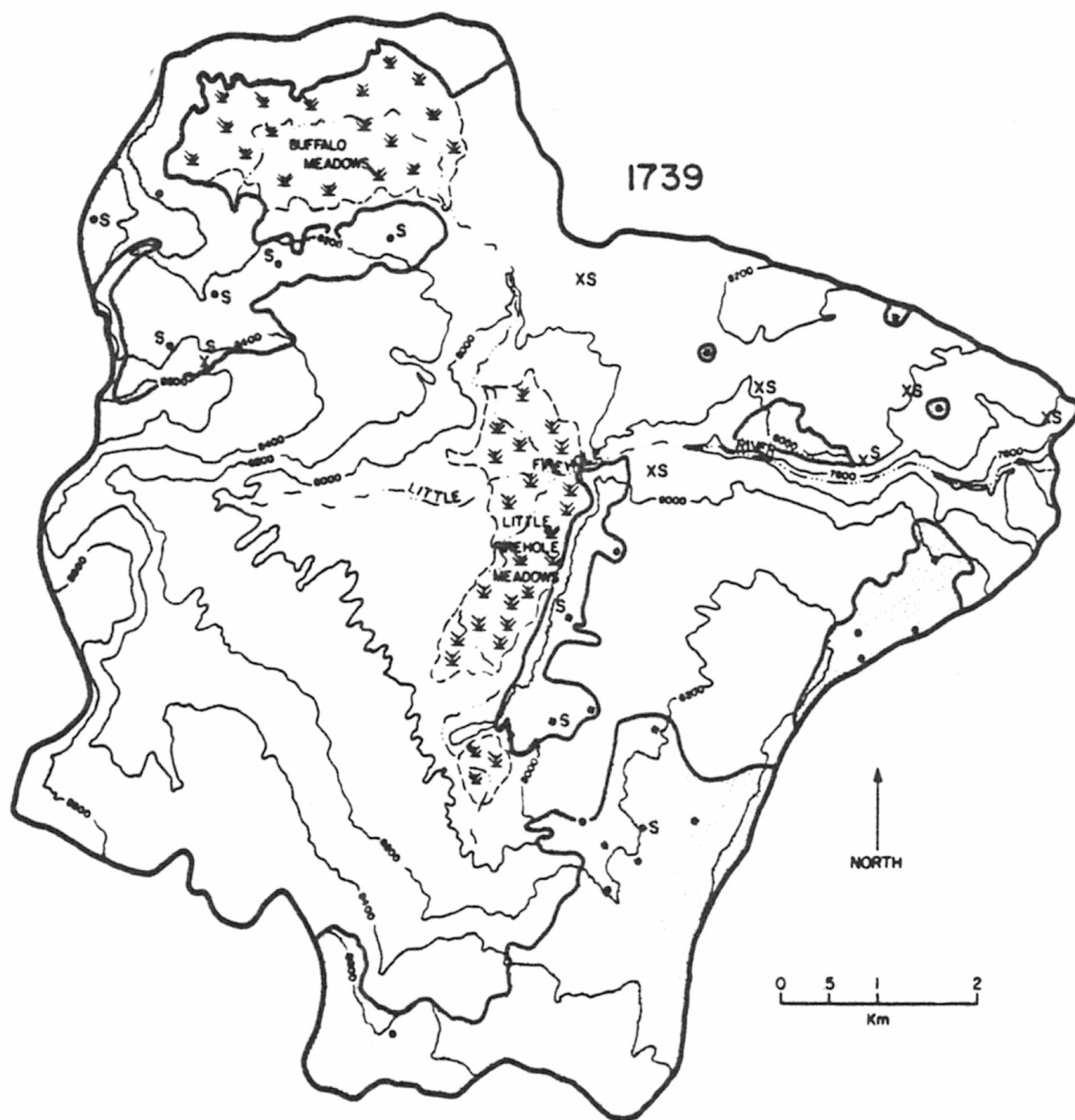


Figure 1-7. Areas burned by the major fire in 1739. ●S = fire scar plus even-aged lodgepole pine reproduction; XS = fire scar without even-aged pine reproduction; ● = even-aged pine reproduction without fire scars.

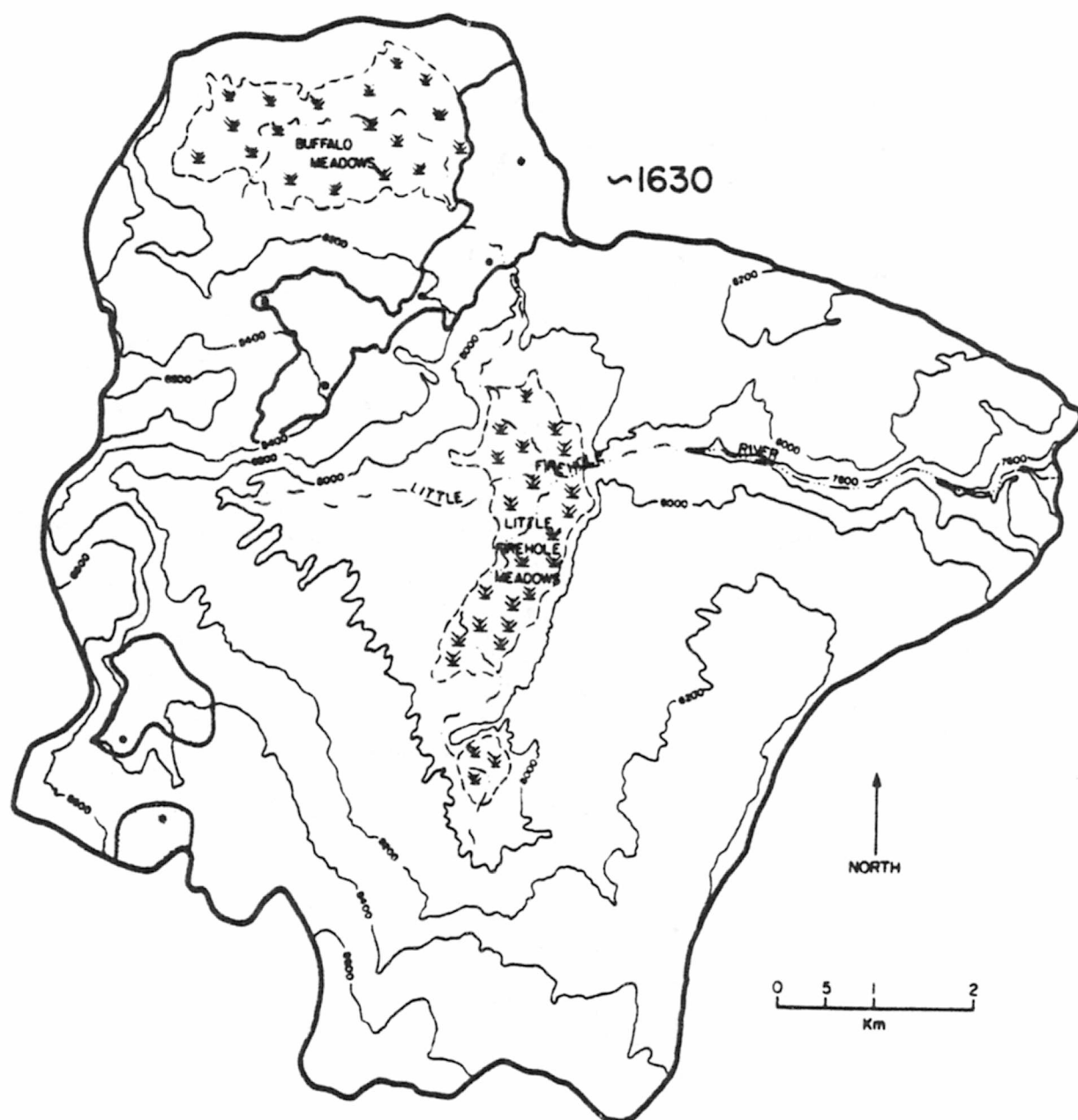


Figure 1-8. Areas burned by the major fire around 1630. ● = even-aged lodgepole pine reproduction without fire scars.

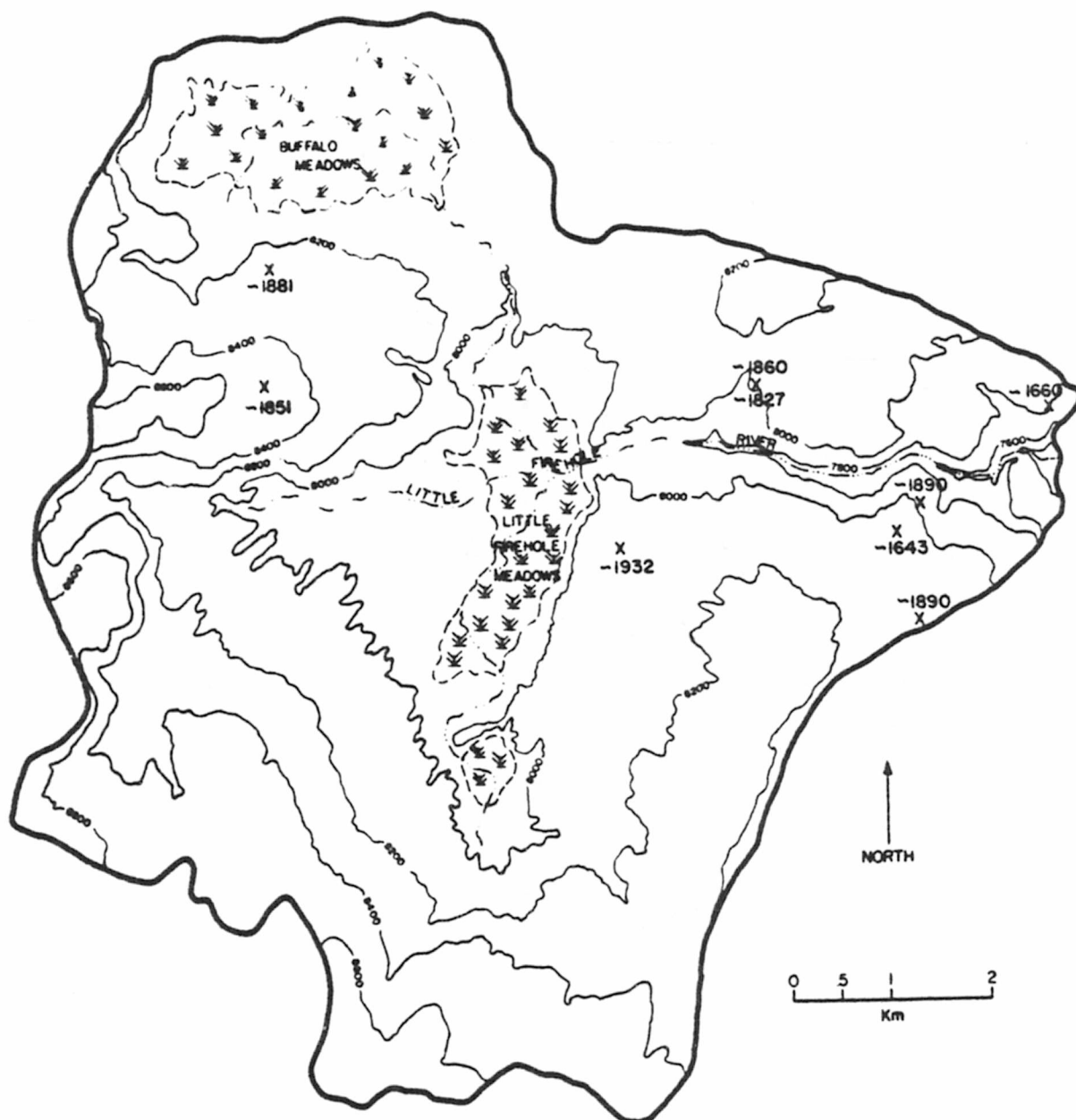


Figure 1-9. Very small fires documented for the Little Firehole River Watershed. These appear to represent isolated lightning strikes that burned less than 1 ha and produced no significant changes in vegetation structure or composition.

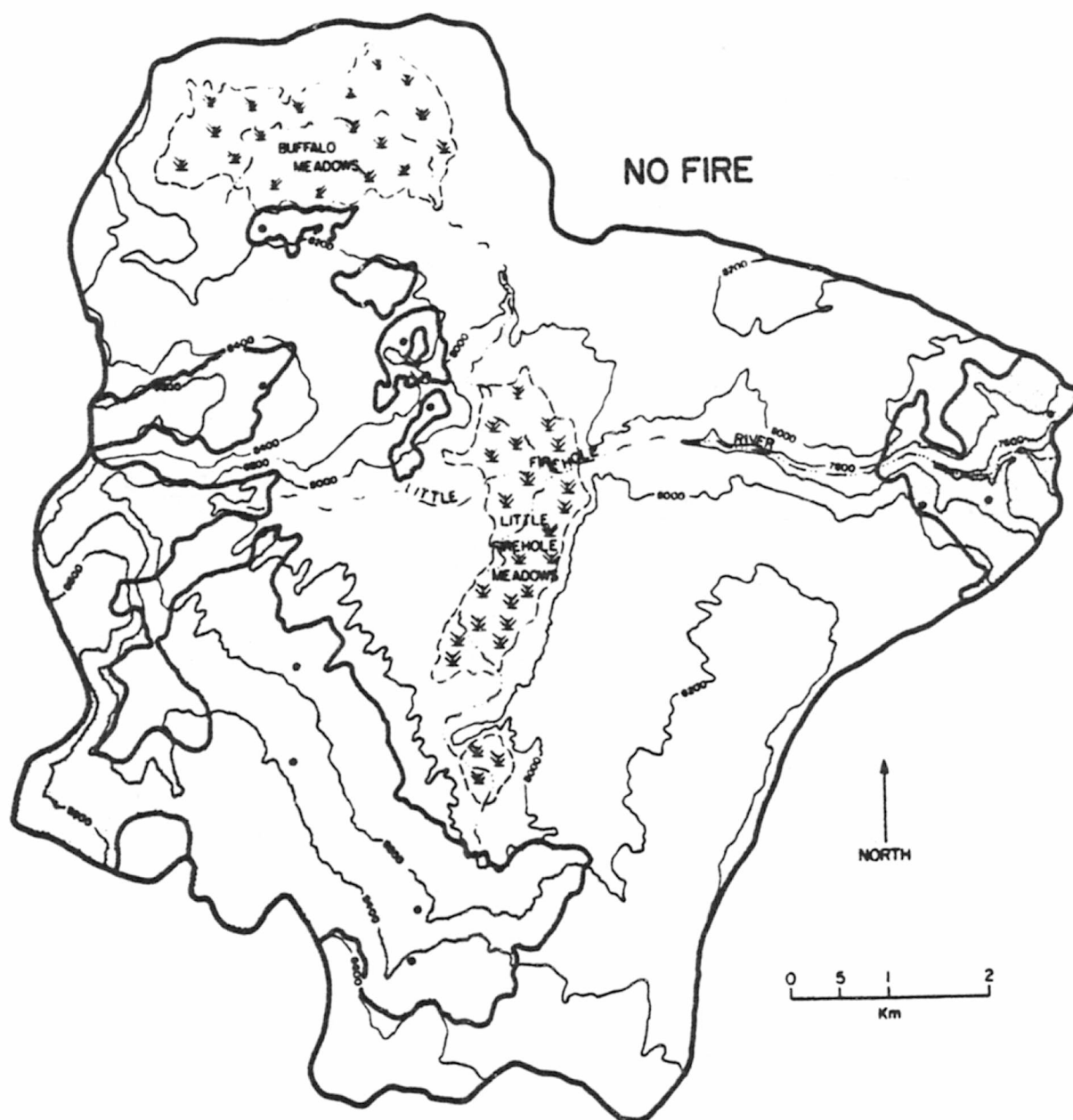


Figure 1-10. Areas on the Little Firehole River Watershed having no evidence of major fire since 1600 (closed circles indicate sample stands). Occasional fire-scarred trees may be found in these areas, but they appear to represent isolated lightning strikes that burned less than 1 ha and produced no significant changes in vegetation structure or composition.

APPENDIX 2

ADDITIONAL FUELS DATA,
STATISTICAL ANALYSES,
AND
RESULTS OF ROTHERMEL'S
FIRE BEHAVIOR SIMULATION MODEL

Table 2-1. Summary of regression analyses on fuels data. See also Fig. 2 - 5 (main text) and Fig. 2-1 - 2-5 (App. 2).

FUEL COMPONENT	STAND AGE INTERVAL	VARIABLES	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
1-HR TL ^{1/} (kg/ha)	0-200	A ^{2/}	1, 5 ^{3/}	12.74	97.5	.85	.72	Y=181+2.50 A ^{4/}
	200-600	A	1, 7	11.37	97.5	.79	.62	Y=772-0.78 A
	200-600	A, S	2, 6	5.65	95	.81	.65	Y=895-0.69 A-2.99 S
10-HR TL (kg/ha)	0-100	A	1, 1	7.80	75	.94	.89	Y=2609-19.94 A
	100-200	A	1, 2	18.49	90	.95	.90	Y=-638+16.69 A
	100-200	A, S	2, 1	28.40	75	.99	.98	Y=-371+19.87 A -13.79 S

^{1/} Fuel Components: See Table 2-2 (App. 2) and Table 2 (main text)

^{2/} Variables: A = stand age S = site index

^{3/} Degrees of Freedom: Regression, Error

^{4/} Regression Equation: Y = fuel mass (kg/ha) or depth (mm)

Table 2-1 (cont.). Summary of regression analyses on fuels data. See footnotes on p. 114.

FUEL COMPONENT	STAND AGE INTERVAL	VARIABLES	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
10-HR TL (kg/ha) (cont.)	200-600	S	1, 7	0.38				
100-HR TL (kg/ha)	0-100	A	1, 1	1.75	95	.99	.99	Y=9145-90.83 A
	100-200	A	1, 2	1.54				
	200-600	S	1, 7	1.48				
1000-HR TL SOUND (kg/ha)	0-150	A	1, 3	5.83	90	.81	.66	Y=38650-314.52 A
	0-150	A, S	2, 2	9.69	90	.95	.91	Y=97440-448.40 A -798.03 S
	150-350	A	1, 5	15.60	97.5	.87	.76	Y=-23188+178.48 A
	150-350	A, S	2, 4	6.31	90	.87	.76	Y=-19440+177.15 A -63.02 S
	350-600	A	1, 4	1.45				

Table 2-1 (cont.). Summary of regression analyses on fuels data. See footnotes on p.114.

FUEL COMPONENT	STAND AGE INTERVAL	VARIABLES	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
1000-HR TL ROTTEN (kg/ha)	0-150	A	1, 3	17.79	97.5	.93	.86	Y=20031-151.33 A
	150-450	A	1, 8	6.03	95	.66	.43	Y=-6364+93.13 A
	450-600	A	1, 1	5.30				
1000-HR TL TOTAL (kg/ha)	0-150	A	1, 3	9.28	90	.87	.76	Y=58681-465.85 A
	0-150	A, S	2, 2	7.83	75	.94	.89	Y=118063-601.09 A -806.085
	150-350	A	1, 5	13.44	97.5	.85	.73	Y=-41269+325.66 A
	150-350	A, S	2, 4	6.76	90	.88	.77	Y=-8916+314.17 A -544.01 S
	350-600	S	1, 4	3.62	75	.69	.47	Y=-37916+1665.71 S
	350-600	S, A	2, 3	3.19	75	.82	.68	Y=2530+1901.07 S -125.35 A
TOTAL FUELS (kg/ha) 1-HR TL 10-HR TL	0-150	A	1, 3	8.79	90	.86	.75	Y=67113-510.94 A
	0-150	A, S	2, 2	6.55	75	.93	.87	Y=130382-655.03 A -858.85 S

Table 2-1 (cont.). Summary of regression analyses on fuels data. See footnotes on p.114.

FUEL COMPONENT	STAND AGE INTERVAL	VARIABLES	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
TOTAL FUELS (kg/ha) (cont.) 100-HR TL 1000-HR TL	150-350	A	1, 5	10.54	97.5	.82	.68	Y=-27496+302.09 A
	150-350	A, S	2, 4	6.31	90	.87	.76	Y=15353+286.88 A -720.48 S
	350-600	S	1, 4	4.21	75	.72	.51	Y=-30992+1656.75 S
	350-600	S, A	2, 3	3.56	75	.84	.70	Y=6345+1874.01 S -115.71 A
TOTAL FUELS EXCLUDING 1000-HR TL SOUND (kg/ha)	0-100	A	1, 1	67.36	90	.99	.99	Y=37076-350.61 A
	100-450	A	1, 10	13.53	99.5	.76	.57	Y=-5080+107.62 A
DUFF DEPTH (mm)	0-600	A	1, 14	14.67	99.5	.72	.51	Y=13.72+0.056 A
	0-600	A, S	2, 13	7.54	99	.73	.54	Y=3.13+0.058 A +0.18 S
NEEDLE LITTER DEPTH (mm)	0-200	A	1, 5	9.42	95	.81	.65	Y=3.74+0.085 A
	0-200	A, S	2, 4	3.80	75	.81	.66	Y=5.11+0.084 A -0.021 S

Table 2-1 (cont.). Summary of regression analyses on fuels data. See footnotes on p. 114.

FUEL COMPONENT	STAND AGE INTERVAL	VARIABLES	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
NEEDLE LITTER DEPTH (cont.)	200-600	S	1, 7	10.42	97.5	.77	.60	Y=31.11-0.35 S
	200-600	S, A	2, 6	6.95	95	.84	.70	Y=30.90-0.42 S +0.011 A
FUEL DEPTH (mm)	0-100	A	1, 1	1.32	90	.99	.99	Y=102-0.89 A
	100-350	A	1, 7	5.82	95	.67	.45	Y=-9.68+0.33 A
	100-350	A, S	2, 6	2.64	75	.68	.47	Y=-36.15+0.33 A +0.51 S
	350-600	A	1, 4	0.69				

Table 2-2. Characteristics of dead, woody fuel components (Brown 1974, Deeming et al. 1977). Timelag refers to how rapidly fuel moisture responds to changes in atmospheric humidity, i.e., the time necessary for a fuel particle to lose approximately 63% of the difference between its initial moisture content and its equilibrium moisture content.

FUEL COMPONENT	UNITS	DESCRIPTION
1-hr Timelag (1-HR TL)	kg/ha	Particles <0.635 cm diameter.
10-hr Timelag (10-HR TL)	kg/ha	Particles 0.635-2.54 cm diameter.
100-hr Timelag (100-HR TL)	kg/ha	Particles 2.55-7.62 cm diameter.
1000-hr Timelag sound (1000-HR TL SOUND)	kg/ha	Particles >7.62 cm diameter; firm, undecomposed wood.
1000-hr Timelag rotten (1000-HR TL ROTTEN)	kg/ha	Particles >7.62 cm diameter; in early stages of decomposition, form still easily recognizable.
Duff Depth	mm	Decomposed organic matter, origin unrecognizable, located above mineral soil and below needle litter.
Needle Litter Depth	mm	Undecomposed needles, twigs, cone scales, and other small material on the forest floor.
Fuel Depth	mm	Average height of fallen, dead, woody material above duff layer.

Table 2-3. Summary of regression analyses of sample variance (s^2) in 20 fuel transects (planar intercept method, Brown 1974) with stand age.

FUEL COMPONENT	STAND AGE INTERVAL	DEGREES OF FREEDOM	F	SIGNIFICANCE LEVEL (%)	r	r ²	REGRESSION EQUATION
1-HR TL ^{1/}	0-600	1, 13 ^{2/}	5.64	95	.55	.30	Y = 39.71 + 0.16 A ^{3/}
10-HR TL	0-600	1, 13	4.48	90	.51	.26	Y = 3.02 + 0.014 A
100-HR TL	0-600	1, 13	0.48				
1000-HR TL SOUND	0-600	1, 13	1.27				
1000-HR TL ROTTEN	0-600	1, 13	4.55	90	.51	.26	Y = -1046 + 42 A
DUFF DEPTH	0-600	1, 13	7.32	97.5	.60	.36	Y = 0.15 + 0.002 A
NEEDLE LITTER DEPTH	0-600	1, 12	7.48	97.5	.62	.38	Y = 0.06 + 0.0003 A
FUEL DEPTH	0-600	1, 11	3.14	75	.47	.22	Y = 4.51 + 0.06 A

^{1/} Fuel Components: See Table 2-2 (App. 2) and Table 2 (main text).

^{2/} Degrees of Freedom: Regression, Error

^{3/} Variables: Y = sample variance in 20 transects
A = stand age

Table 2-4. Results of Rothermel's (1972) fire behavior simulation model using data from two upland forest stands on the Little Firehole River Watershed (Table 2-5). The model assumes a homogeneous fuel bed and restriction of the fire to surface fuels only, i.e. the fire does not enter the canopy (Albini 1976). Explanations of the model parameters are as follows:

Windspeed at midflame height: these values were entered arbitrarily to reflect the entire range of possible windspeeds on the forest floor (corresponding windspeeds above the canopy would be much greater).

Rate of spread: rate of forward movement of the fire edge, computed as in Rothermel (1972).

Byram's intensity: a measure of heat release per unit time along a unit length of the fire edge, computed according to Byram (1959).

Byram's flame length: flame length, an estimate based on fire intensity (Byram 1959).

Van Wagner's crown scorch height: height of lethal scorching, an estimate based on fire intensity (Van Wagner 1973; cited in Albini 1976).

P. Thomas equations for flame: flame parameters estimated according to Thomas (1963) (cited in Albini 1976).

Table 2-4. (Continued)

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I. Stand 22 (Abla/Vasc HT; 450 yr old)

	WINDSPEED (MPH) AT MIDFLAME HEIGHT				
	0.0	2.0	4.0	6.0	8.0
Rate of spread (ft/min)	0.73	2.31	4.51	7.03	9.78
Byram's intensity (BTU/sec/ft)	7.7	24.6	48.0	74.9	104.2
Byram's flame length (ft)	1.2	2.0	2.7	3.3	3.8
Van Wagner's crown scorch height (ft) on a 77°F day	3.9	7.3	8.6	8.9	9.0
P. Thomas equations for flame					
Length (ft)	0.9	1.3	1.7	2.1	2.5
Height (ft)	0.9	0.7	0.7	0.8	0.9
Horizontal reach (ft)	0.0	1.1	1.5	2.0	2.3
Tilt angle from vertical (degrees)	0.0	56.4	64.0	67.3	69.3

II. Stand 66 (Pico/Cage HT, 350 yr old)

	WINDSPEED (MPH) AT MIDFLAME HEIGHT				
	0.0	2.0	4.0	6.0	8.0
Rate of spread (ft/min)	0.87	2.63	5.30	8.48	12.04
Byram's intensity (BTU/sec/ft)	5.2	15.8	31.8	50.8	72.2
Byram's flame length (ft)	1.0	1.6	2.2	2.7	3.2
Van Wagner's crown scorch height (ft) on a 77°F day	3.0	5.1	5.7	5.9	6.0
P. Thomas equations for flame					
Length (ft)	0.7	0.9	1.2	1.5	1.8
Height (ft)	0.7	0.4	0.5	0.5	0.6
Horizontal reach (ft)	0.0	0.7	1.1	1.4	1.7
Tilt angle from vertical (degrees)	0.0	58.7	65.5	68.5	70.3

Table 2-5. Characteristics of two upland forest stands on the Little Firehole River Watershed that were treated in Rothermel's (1972) fire behavior simulation model.

	STAND	
	22	66
Habitat type	Abla/Vasc	Pico/Cage
Approximate age	450	350
1-HR TL fuels (tons/acre)	0.220	0.254
10-HR TL fuels (tons/acre)	0.813	0.737
100-HR TL fuels (tons/acre)	1.073	1.392
Average depth of undecomposed needle litter (inches)	0.49	0.53
Live fuels (tons/acre, dry wt)	0.8	0.1
Dead tissue in live fuels (%)	10-20	30-40
Major live fuel components (% ground cover)		
<u>Vaccinium scoparium</u>	80	<5
<u>Carex geyeri</u>	5	15
dry moss	20	30
<u>Arnica cordifolia</u> and <u>Hieracium</u> <u>albiflorum</u>	5	0
<u>Lupinus argenteus</u>	0	5
other species	<5	<5

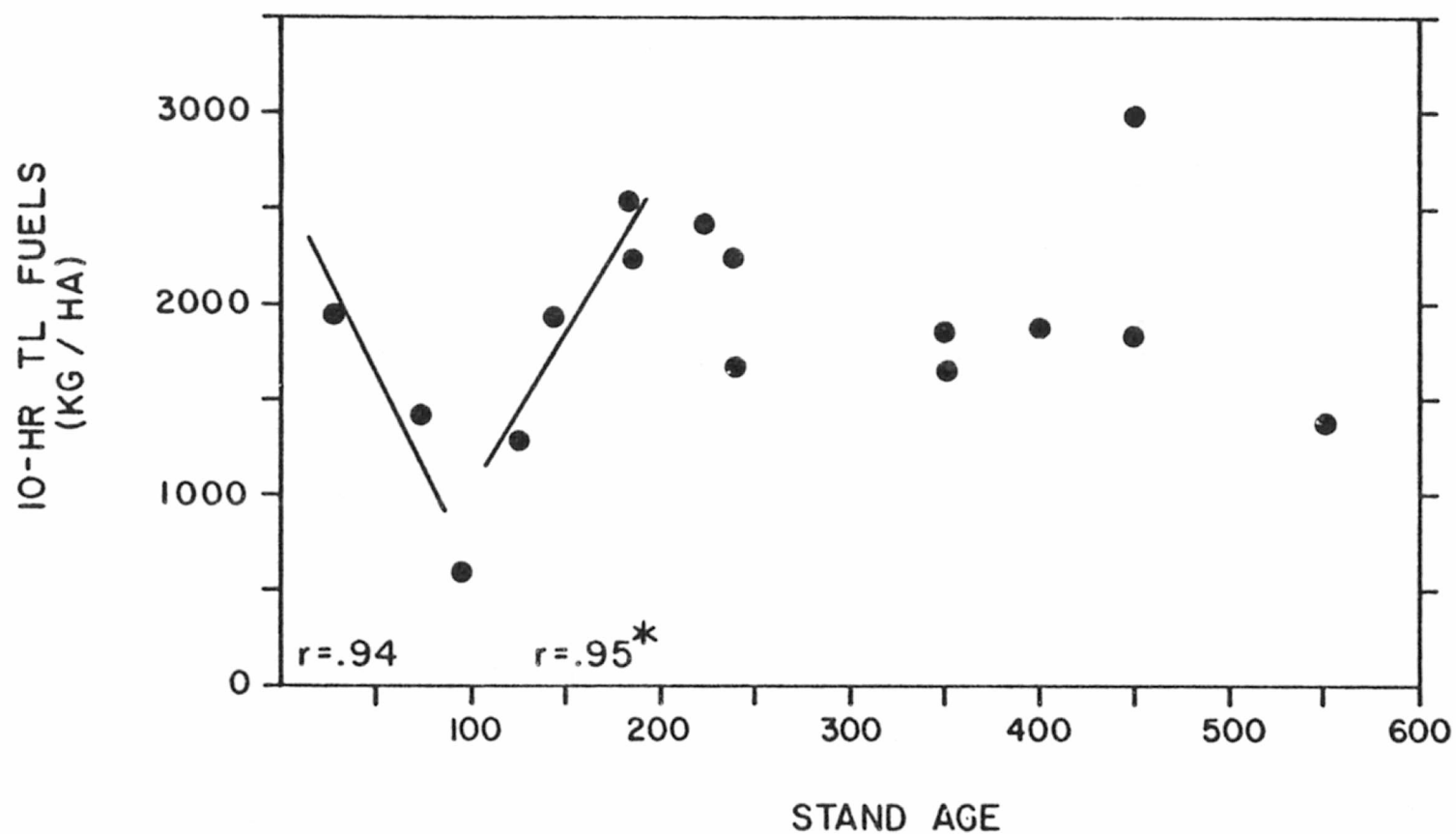


Figure 2-1. Changes in 10-HR TL fuels (Table 2-2) along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (* = 90% significance level; no superscript = 75%).

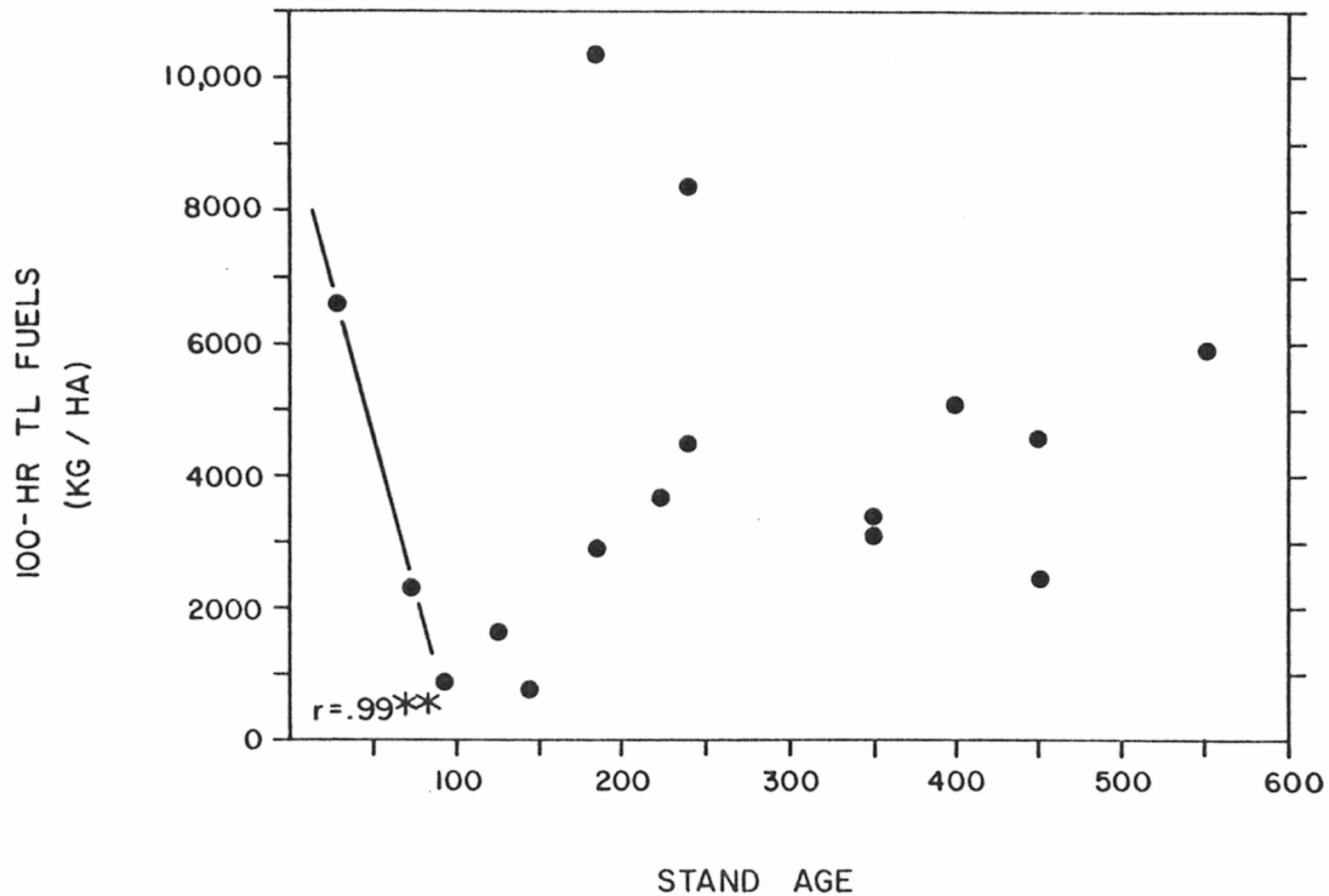


Figure 2-2. Changes in 100-HR TL fuels (Table 2-2) along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for the stand age interval where the slope is significantly non-zero (** = 95% significance level).

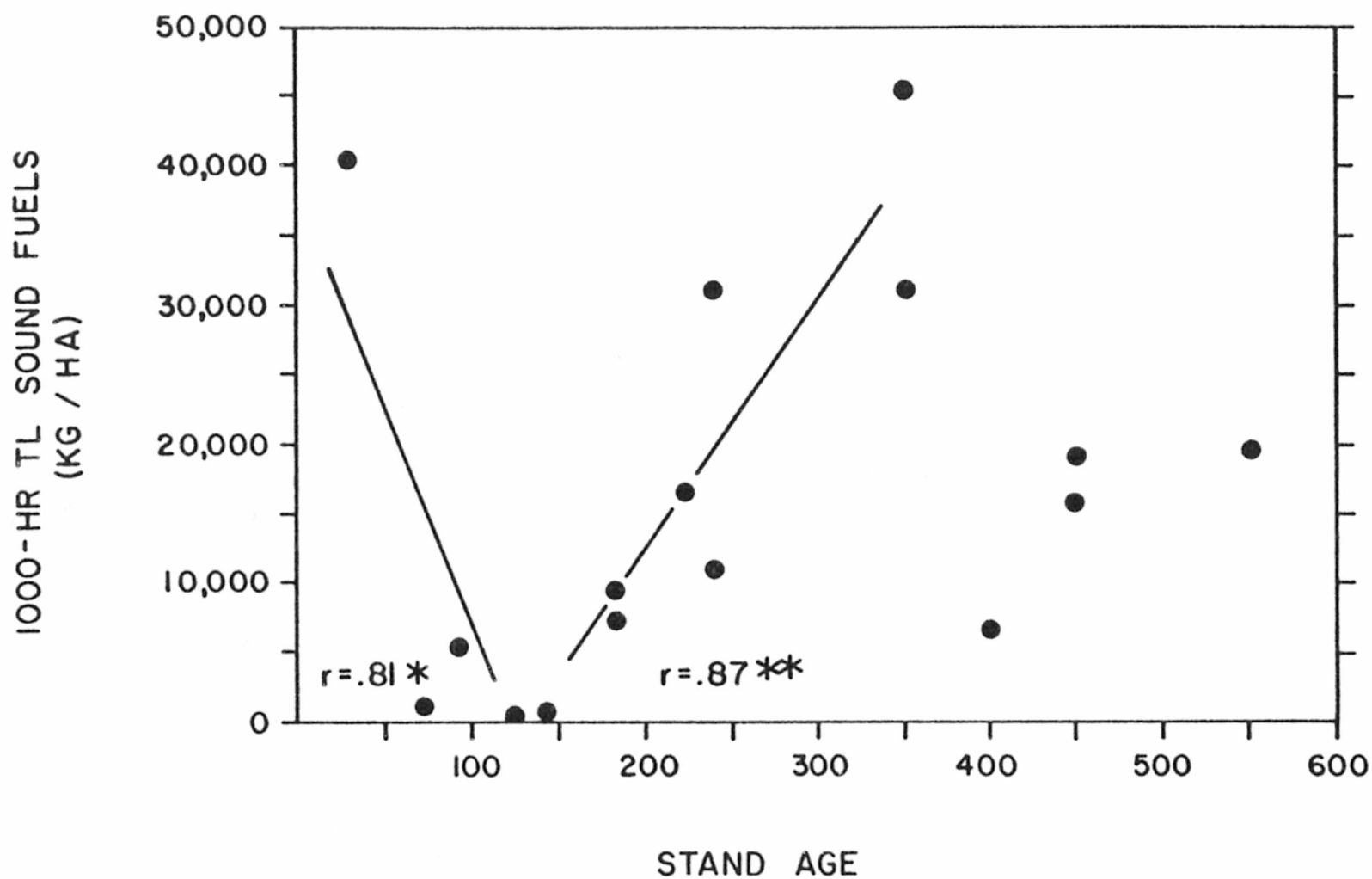


Figure 2-3. Changes in 1000-HR TL sound fuels (Table 2-2) along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (* = 90% significance level; ** = 95%).

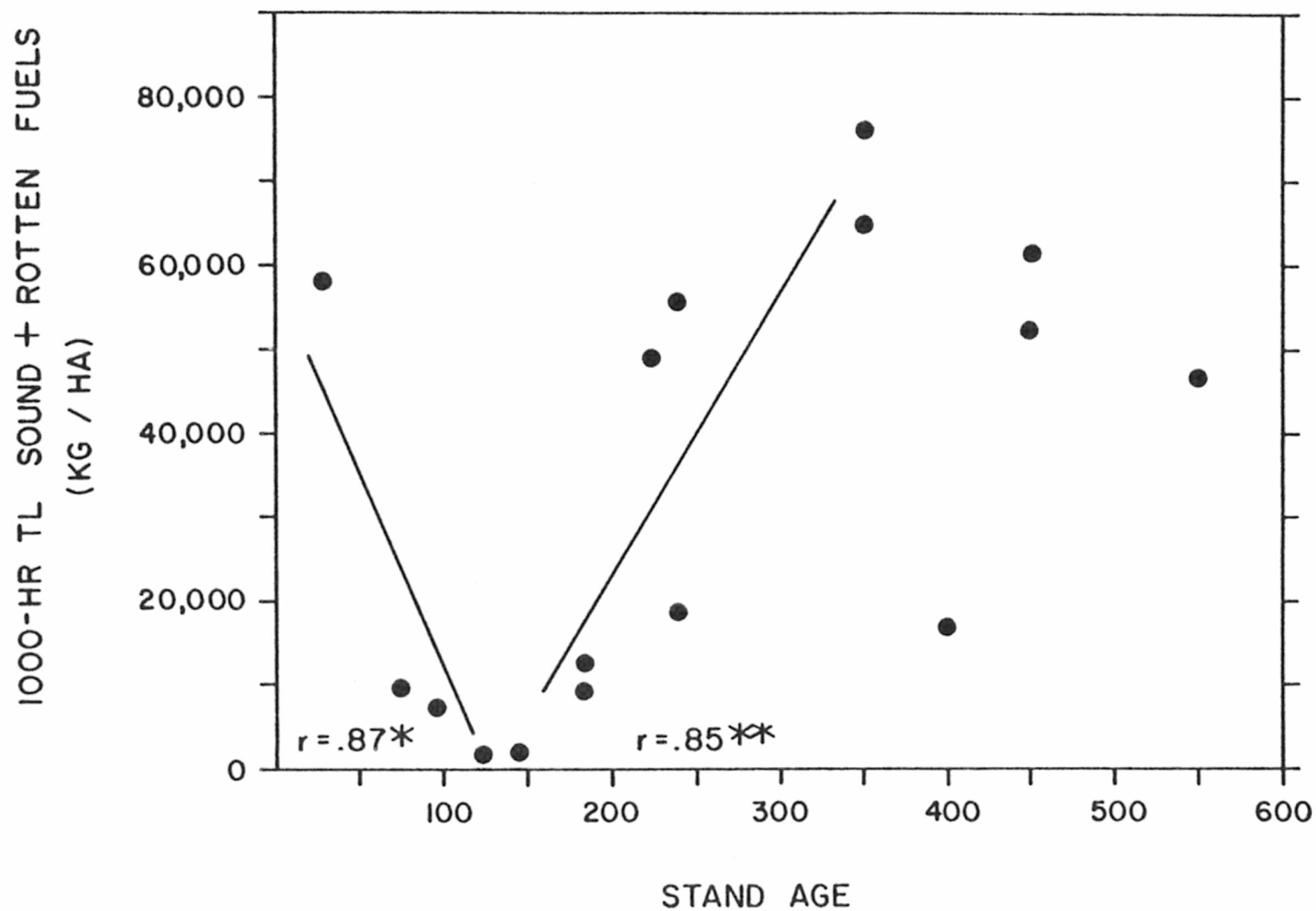


Figure 2-4. Changes in total 1000-HR TL fuels (Table 2-2) along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (* = 90% significance level; ** = 95%).

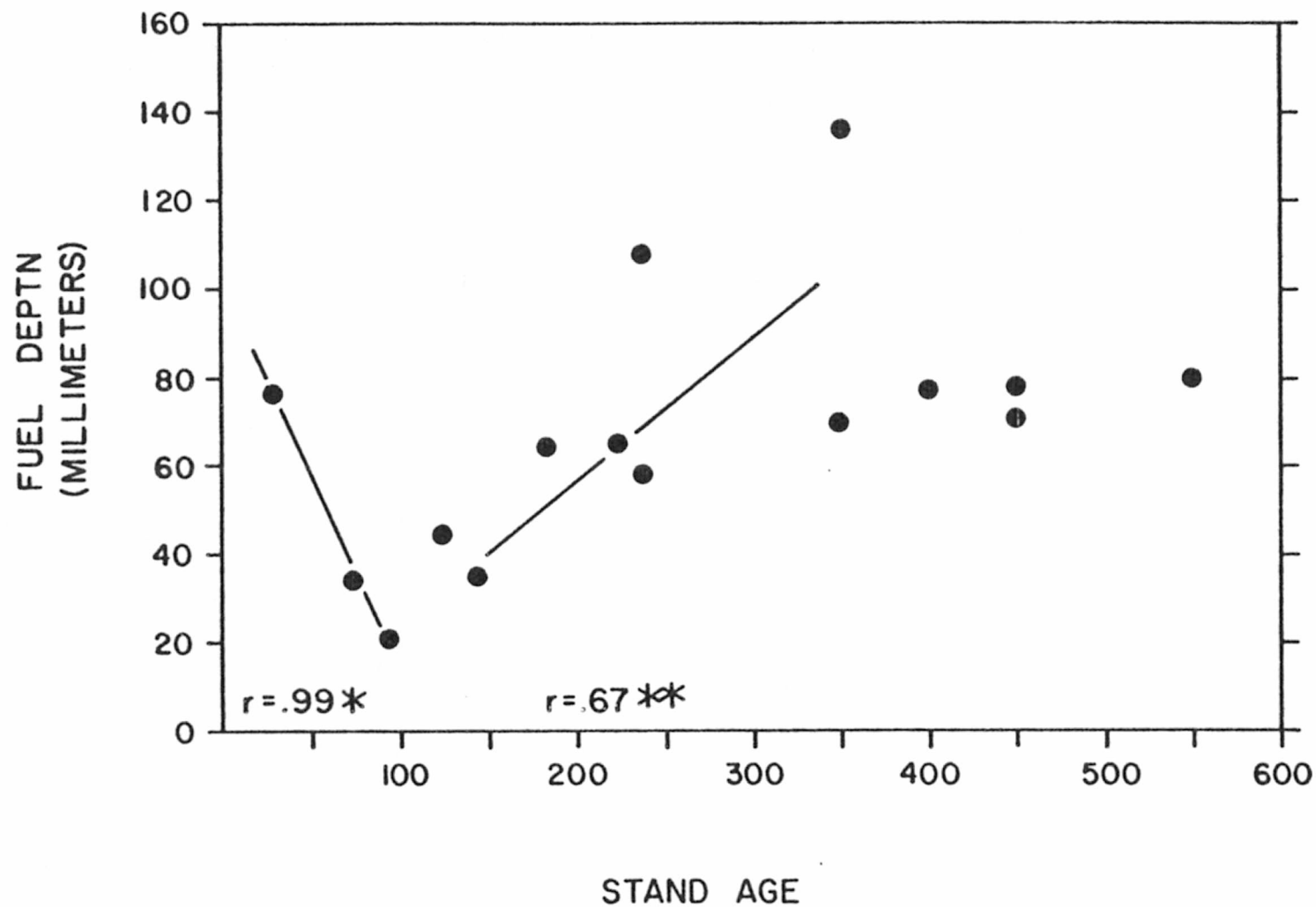


Figure 2-5. Changes in fuel depth (Table 2-2) along a chronosequence of upland forest stands. The regression line and correlation coefficient are shown for stand age intervals where the slope is significantly non-zero (* = 90% significance level; ** = 95%).

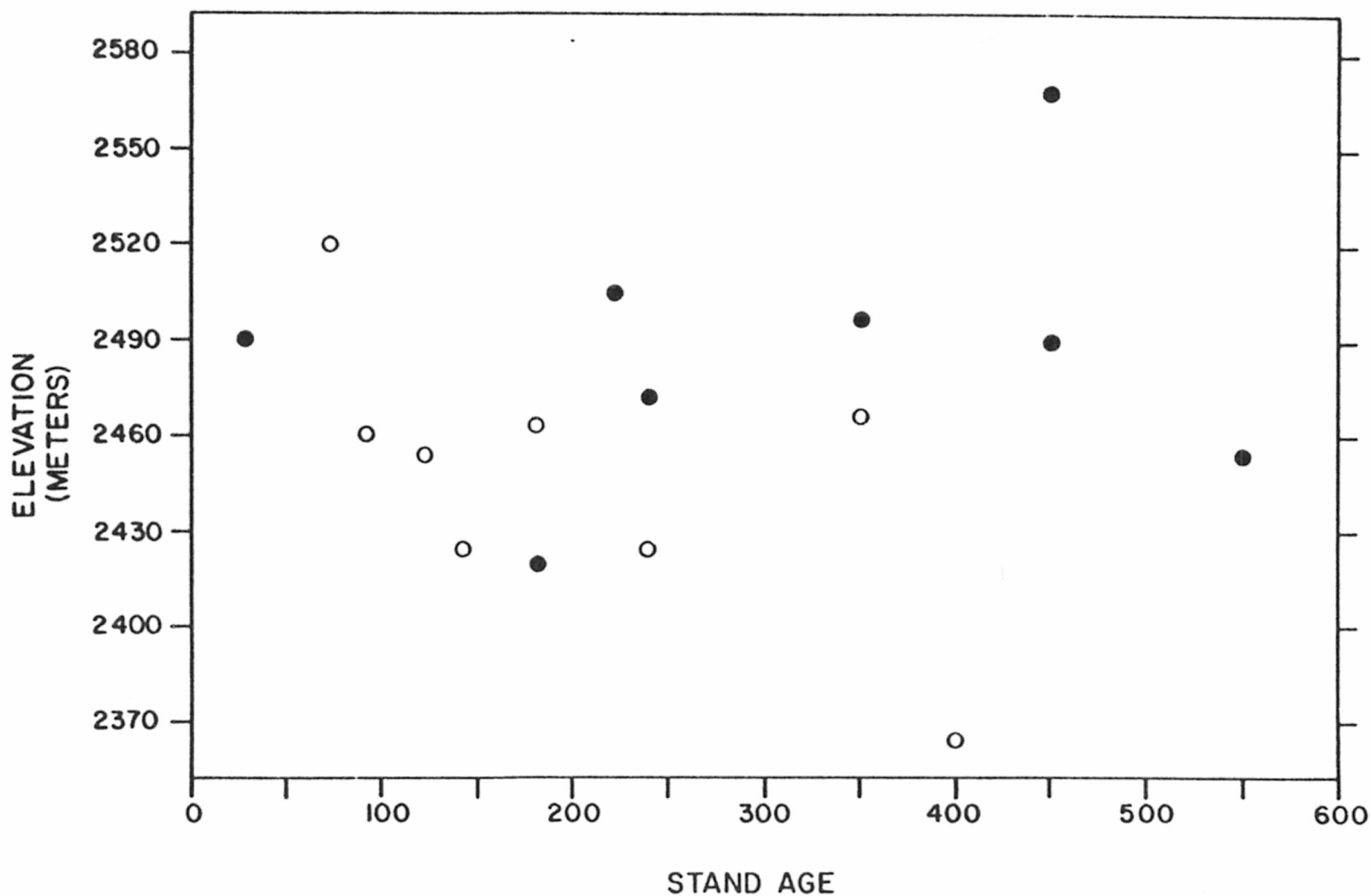


Figure 2-6. Elevation vs. stand age for the 16 stands in which fuels were sampled, showing no apparent relationship between stand age and elevation. Closed points represent the Abia/Vasc habitat-type; open points represent the Pico/Cage habitat-type.

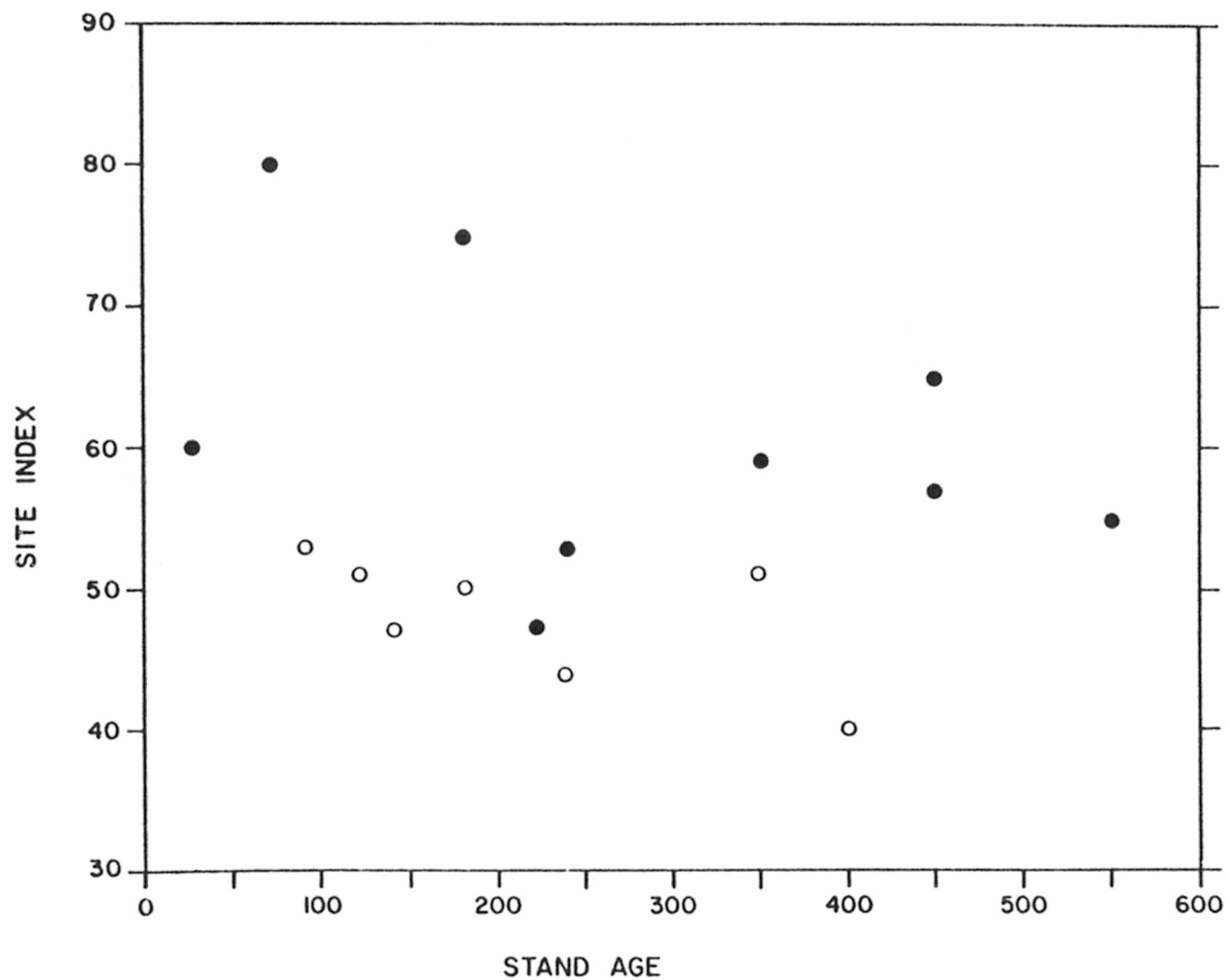


Figure 2-7. Site index vs. stand age for the 16 stands in which fuels were sampled, showing no apparent relationship between site index and stand age. Closed points represent the Abl/Vasc habitat-type; open points represent the Pico/Cage habitat-type.

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- Thomas, P. H. 1963. The size of flames from natural fires, p. 884-859, in: Proceedings of the Ninth International Symposium on Combustion (1962). Academic Press Inc., New York. (cited in Albini 1976).
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APPENDIX 3

COMPUTER SIMULATION MODEL
OF
FOREST SUCCESSION
AND
LANDSCAPE DIVERSITY

This program, written in structured FORTRAN, was designed to simulate forest succession and landscape diversity on the Little River Watershed in Yellowstone National Park. However, it is sufficiently flexible to be used for other landscapes with different disturbance histories and rates of succession provided that the following conditions are met: (1) five habitat-types (HT) (or vegetation-types) are treated, two of which are subdivided into six or fewer successional stages on the basis of stand age; and (2) fire or other perturbations being simulated completely destroy an existing community and return the site to the earliest successional stage. Any number of disturbance events affecting any portion of the landscape may be simulated, and the definitions of habitat-types and successional stages may be changed to represent the landscape of interest. For landscapes containing a different number of habitat-types and/or more than six successional stages, the program may still be applicable with some minor revisions. Table 3-1 contains definitions of all variables used in the program.

The landscape is treated as a matrix with I rows and J columns. Each cell in the matrix represents a 5-ha stand in my study, though it could represent an area of any size. There actually are five superimposed matrices containing five different kinds of information about each cell. The matrix AGE contains stand age. The matrix VEGETYPE contains numbers from 1 - 5 indicating the habitat-type of each cell (Table 3-2). To increase the number of habitat-types it would be necessary to add some decision statements in the

classification algorithm (discussed below). The matrix COMMTYPE contains the classification of each cell as used in computing landscape diversity indices. As discussed in the main text, there are 10 taxa recognized by this classification because the two upland forest HTs are not distinguished in early and middle successional stages, although they are distinguished in the climax stage (Table 3-3). The matrix STATE contains the classification of each cell as used in computing the proportion of the landscape covered by forests in various successional stages. For this the two upland HTs are distinguished in all stages, resulting in a total of 15 taxa (Table 3-3). The matrix SEREINDX contains numbers from 1 - 7 indicating which of seven possible rates of succession characterizes each cell (Tables 3-4 and 3-5). More or fewer than seven successional rates can be used by modifying this matrix and the matrix SERE (discussed below). The data in the matrices AGE, SEREINDX, and VEGETYPE are empirical, and must be input at the beginning of the program. Data in the matrices COMMTYPE and STATE are supplied by decision statements and calculations within the program. These data are then used to compute landscape diversity indices and other summarizations comprising the program output.

Programming constraints necessitate data for every cell in the matrices described above. Obviously, however, many landscape units are not precisely rectangular in shape. This problem is overcome by constructing matrices large enough to encompass the landscape unit, then initially assigning a negative stand age to

all cells lying outside the unit's boundaries. The program will assign values of zero in the matrices COMMTYPE and STATE for all cells having negative stand ages, and these cells will be ignored in all computations of landscape diversity indices and other program output. The cells having negative stand ages may be assigned any value in the matrices SEREINDX and VEGETYPE because these data will be ignored. In constructing a matrix to encompass the landscape unit of interest, the first row and the first column must lie outside the unit's borders (i.e., must be assigned a negative stand age) to allow computation of the patchiness diversity index (described below). Matrix size is indicated by the variables ROWSIZE and COLSIZE. I used a 50 x 49 matrix, i.e. ROWSIZE = 50 and COLSIZE = 49. If a matrix of a different size is to be used, the dimensions of the matrices AGE, SEREINDX, VEGETYPE, COMMTYPE, and STATE must also be modified in all declaration statements.

The program begins by calling the subroutine DATAFILL which inputs all preliminary data from four data files (Table 3-6). To simplify the input of the large amount of data needed to fill the matrices AGE, SEREINDX, and VEGETYPE, the program first initializes all cells in these three matrices with the value of zero. For the matrix AGE, the coordinates and stand age of certain cells are then read from input file no. 106, these new values replacing the zeros assigned previously. Because many adjacent cells are to be of the same age when the matrix is filled, this input file contains only the ages of the cells at the beginning of each row and those cells

with a different stand age than the cell in the preceding column of the same row. Each line in the file contains the coordinates and stand age of one cell; there may be any number of lines depending on the complexity of the stand age mosaic within the landscape. The program then proceeds sequentially, row by row, through all cells in the matrix; every cell still having a value of zero is assigned the value of the cell in the preceding column of the same row. Similarly, the coordinates and index values (discussed below) for selected cells in the matrix SEREINDX are read from file no. 107, then the matrix is filled by the same procedure used for the matrix AGE. Finally, the matrix VEGETYPE is filled in the same manner using data from file no. 109.

After completion of the subroutine DATAFILL, the program initializes the counter variable M (discussed below) and sets the year (the variable YEAR) equal to the first year to be simulated (the variable FIRSTYR, the value of which is input from file no. 105; e.g. 1778). The program then enters a loop which eventually will be terminated when YEAR exceeds the selected end point in the simulation (the variable YRLIMIT, input from file no. 105; e.g. 1978).

Upon entering the loop, the program first determines whether any fires have occurred since the last simulated year. This decision is based on the fire-years input from file no. 105 (array FIREYEAR). If fire has occurred, data indicating the area burned are read from one of four additional input files numbered 121, 122,

123, and 124. The appropriate file is selected according to the counter, M ; i.e. for the first fire, $M = 1$ and the data file number is $(120 + M) = 121$. If the program is to be run with less than four fires, e.g. with only two fires, the last two fire-years in the array FIREYEAR should be dates that the simulation will never reach (e.g. 9999). If no fires are to occur, all of the fire-years should be 9999. More than four fires may be simulated by making appropriate changes in the dimensions of the array FIREYEAR in the declaration statements and by changing the character sequence 'IF((M.LT.5)....' to 'IF((M.LT.X)....' where X equals the number of fires plus one. Each line in input files 121, 122, etc. contains the coordinates of the first cell burned in a row plus the column of the last contiguous cell burned in that row. For example, if columns 6 - 10 in row 23 all burned, a line in the file would be: 23, 6, 10. There may be any number of lines in each file.

After initializing several counter variables to be used later in computing landscape diversity indices, the program enters a second loop (contained within the first loop) in which it sequentially analyzes each cell in the landscape matrix, proceeding row by row. The program first determines whether a particular cell lies within the landscape boundaries (i.e., has a non-negative stand-age). If the cell is within the boundaries, a series of decision statements follows which classifies the cell and assigns it values in the matrices STATE and COMMTYPE. An appropriate element in the counter array COMMUNITY is also assigned a value

for use later in computing landscape diversity. The first three decision statements in the series determine whether the cell belongs to one of the three habitat-types not having successional stages (Table 3-3). For the two habitat-types having successional stages, cell classification is based on habitat-type and stand age, according to seral stage endpoints contained in the matrix SERE (Table 3-5). The rows in the matrix contain stand ages associated with the six successional stages recognized in the study (Table 3-3), the appropriate column being indicated by the cell's value in the matrix SEREINDX. Fewer than six successional stages may be treated by assigning zeros to the bottom rows in the matrix SERE; e.g. to treat only three successional stages, rows 3, 4, and 5 would be filled with zeros. To treat more than six stages, additional rows would be needed in the matrix SERE plus additional decision statements in the program.

After classifying a particular cell, the program assigns values to several counter variables to be used in computing landscape diversity indices. The counter array CELL, used in the patchiness index (see below), stores the classification of the two adjacent cells in the (I-1,J) and (I,J-1) positions. The relative dissimilarity between these adjacent cells and the cell presently being analyzed is determined from the matrix PATINDEX (Table 3-7), with the value being stored in the counter PATCHSUM. This dissimilarity value is zero for a cell lying adjacent to another cell with the same classification or a cell classified as COMMTYPE zero

(i.e. lying outside the boundary of the landscape). The greatest possible dissimilarity value that could be assigned to a single cell is 2.0 (i.e., a value of 1.0 with each of two adjacent neighbors within the landscape boundary), this maximum value being added to the counter variable PATCHMAX. If the cell is adjacent to one cell lying within and another lying outside the landscape boundary, PATCHMAX is increased by 1.0. If both adjacent cells lie outside the boundary, PATCHMAX is not changed. Finally, the stand age of the cell (matrix AGE) is increased by an amount specified by the variable INCREMNT and the program moves to the next cell.

After all cells in the landscape matrix have been classified, the program calls the subroutine INDICES to compute landscape diversity indices (Table 3-8). The maximum possible evenness value for the number of community-types present in the landscape is computed by an additional subroutine MAXEVEN, for which it is necessary to input the proportion of the landscape occupied by each of the five habitat-types (variables PICOAREA, ABLAAREA, RIPFAREA, SLOPAREA, MEADAREA). These data may not be readily available. However an easy way to obtain the data is to enter dummy values for these variables and run the program for a one-year simulation (i.e. FIRSTYR = YRLIMIT). The output contains the proportion of the watershed occupied by each habitat-type (discussed below). These values then can be entered in place of the dummy values and the program re-run for an accurate calculation

of the evenness index.

After execution of the subroutine INDICES, the program prints the results (Table 3-9). An optional part of the output is a map of the landscape created by printing the matrix STATE. This map is particularly useful for comparing the computer-simulated landscape with empirical maps or aerial photographs of the landscape to identify errors or necessary modifications in the preliminary empirical data input. The map is printed at intervals specified by the variable MAPYR, e.g. if MAPYR = 200.0 the map is printed every 200 yr in the simulation. Following data output, the year being simulated is increased according to the value of the variable INCREMNT, and the program returns to the beginning of the first major loop (e.g. if YEAR = 1778 and INCREMNT = 20, YEAR becomes 1798 and the landscape is simulated once again). The program is terminated when YEAR exceeds the endpoint for the simulation specified by the variable YRLIMIT.

Table 3-1. Definitions of variables, arrays, and matrices used in the program.

- ABLAAREA: the proportion of the landscape area occupied by the Abia/Vasc HT (a real number from 0.0 - 1.0)
- ABLANUMB: the number of successional stages in the Abia/Vasc HT present in the landscape being analyzed (an integer from 1 - 6)
- AGE(I,J): stand age, i.e. time since last perturbation that destroyed the stand and initiated secondary succession (a ROWSIZE x COLSIZE matrix, each cell containing an integer)
- CELL(K): the values of adjacent cells (positions (I-1,J) and (I,J-1)) in the matrix COMMTYPE (a K-element array, each element containing an integer from 0 - 11)
- CELLNUMB: the number of cells lying within the boundaries of the landscape unit being analyzed (any positive integer)
- COLSIZE: the number of columns in the landscape matrix (any positive integer)
- COMMTYPE(I,J): community-type (Table 3-3) (a ROWSIZE x COLSIZE matrix, each cell containing an integer from 0 - 10)
- COMMUNITY(K): a counter variable used to compute the richness index (Table 3-8) (a 10-element array, each element representing one of ten respective community-types (Table 3-3) and containing the integer 0 or 1)
- EARLY: the percent of the landscape occupied by early forest successional stages, i.e. community-types 1 and 2 in Table 3-3 (a real number from 0.0 - 100.0)

Table 3-1. (Continued)

ECOUNTER: a counter variable used to compute the evenness index (Table 3-8) (any non-negative real number)

ENDPT: the column of the last cell in a row of contiguous burned cells (any positive integer)

EVENMAX: the maximum possible value of the evenness index (Table 3-8) for the number of community-types present (any positive real number)

EVENNESS: the value of the evenness index (Table 3-8) computed for a particular simulated landscape (any positive real number)

FILENUMB: the number of the input file that specifies the areas burned in a particular fire (any integer greater than 120)

FIREYEAR(K): years in which fires occur in the simulation (a K-element array, each element containing any 4-digit integer)

FIRSTYR: the year in which the simulation begins; i.e. the first year for which a landscape reconstruction is made (any 4-digit integer)

I: a counter variable indicating a row in a matrix (any positive integer)

INCREMNT: the number of years added to the date in each successive landscape simulation (any non-negative integer)

Table 3-1. (Continued)

- INDX: a value read from input file no. 107 and stored in a cell of the matrix SEREINDX to indicate which of seven possible successional rates is applicable (an integer from 1 - 7)
- J: the column number in any two-dimensional matrix (any positive integer)
- K: the element number in any unidimensional array (any positive integer)
- LATE: the percent of the landscape comprised of late forest successional stages (community-types 5, 6, 7; Table 3-3) (a real number from 0.0 - 100.0)
- M: a counter indicating the 1st, 2nd, etc., fire-year incorporated in the landscape simulation (any positive integer)
- MAPYR: the interval (in years) between successive printings of the landscape map (matrix STATE) in the program output (any positive real number)
- MEADAREA: the proportion of the landscape occupied by the meadow habitat-type (a real number from 0.0 - 1.0)
- MIDDLE: the percent of the landscape comprised of middle forest successional stages (community-types 3, 4; Table 3-3) (a real number from 0.0 - 100.0)
- N: an internal counter variable in the DO-LOOP that inputs data on the cells affected by a fire (see text) (any positive integer)

Table 3-1. (Continued)

- NUMBER: stand age, read from input file no. 106 and stored in a cell of the matrix AGE (any integer)
- PATCHMAX: sum of maximum possible dissimilarity values (Table 3-6) between all pairs of adjacent cells in the landscape matrix (any non-negative real number)
- PATCHNES: the value of the relative patchiness index (Table 3-8) (a real number from 0.0 - 100.0)
- PATCHSUM: sum of dissimilarity values (Table 3-7) between all pairs of adjacent cells in the landscape matrix (any non-negative real number)
- PATINDEX(I,J): dissimilarity between adjacent cells composed of various community-types (Table 3-7) (an I x J matrix, each cell containing a real number from 0.0 - 1.0)
- PER(K): the proportion of the landscape composed of each of ten community-types (COMMTYPE, Table 3-3) (a 10-element array, each element containing a real number from 0.0 - 1.0)
- PERCENT(K): the percent of the landscape composed of each of 15 community-types (STATE, Table 3-3) (a 15-element array, each element containing a real number from 0.0 - 100.0)
- PICOAREA: the proportion of the landscape area occupied by the Pico/Cage HT (a real number from 0.0 - 1.0)
- PICONUMB: the number of successional stages in the Pico/Cage HT present in the landscape being analyzed (an integer from 1 - 6)

Table 3-1. (Continued)

RCOUNTER: a counter variable used to compute the richness index
(Table 3-8) (any non-negative integer)

RELEVEN: the value of the relative evenness index (Table 3-8)
(a real number from 0.0 - 100.0)

RICHNESS: the value of the relative richness index (Table 3-8)
(a real number from 0.0 - 100.0)

RIPFAREA: the proportion of the landscape area occupied by
the riparian forest (Abla/Caca) habitat-type (a real
number from 0.0 - 1.0)

ROWSIZE: the number of rows in the landscape matrix (any
positive integer)

SERE(I,J): stand age endpoints demarcating forest successional
stages under different rates of succession (an I x J matrix,
each cell containing any non-negative integer)

SEREINDX(I,J): a number referencing the column in the matrix
SERE that reflects the rate of succession in a particular
cell (a ROWSIZE x COLSIZE matrix, each cell containing any
positive integer)

SLOPAREA: the proportion of the landscape area occupied by
the steep slopes habitat type (a real number from 0.0 - 1.0)

STATE(I,J): Community-type (Table 3-3) (a ROWSIZE x COLSIZE
matrix, each cell containing an integer from 0 - 15)

SUM(K): the number of cells in the landscape matrix classified
as one of 15 community-types (Table 3-3) (a 15-element array,
each element containing any non-negative integer)

Table 3-1. (Continued)

TYPE: habitat-type, read from input file no. 109 and stored in
a cell of the matrix VEGETYPE (an integer from 1 - 5)

VEGETYPE(I,J): habitat-type (Table 3-2) (a ROWSIZE x COLSIZE
matrix, each cell containing an integer from 1 - 5)

YEAR: the current year in which a landscape simulation is
being performed (any 4-digit integer)

YRLIMIT: the last year in which a landscape simulation is
to occur; the program is terminated when YEAR exceeds
this value (any 4-digit integer).

Table 3-2. Key to habitat-types in the matrix VEGETYPE (see section on STUDY AREA in main text for descriptions of habitat-types).

VALUE IN VEGETYPE(I,J)	HABITAT-TYPE OF CELL(I,J)
1	Upland forest (Pico/Cage)
2	Upland forest (Abla/Vasc)
3	Riparian forest (Abla/Caca)
4	Steep slope
5	Meadow

Table 3-3. Community-types recognized in the present study (see section on STUDY AREA in main thesis for more descriptive details).

DESCRIPTIVE NAME					
Habitat Type	Successional Stage	STATE	COMMTYPE	COMMUNITY	VEGETYPE
Meadow	a	10	10	10	5
Steep Slope	a	9	9	9	4
Riparian Forest	a	8	8	8	3
Upland Forest	Climax forest	7	7	7	2
(Abla/Vasc HT)	Transitional forest	15	5	5	2
	Mature pine forest	14	4	4	2
	Immature pine forest	13	3	3	2
	Seedling-sapling stage	12	2	2	2
	Herbaceous stage	11	1	1	2
Upland Forest	Climax forest	6	6	6	1
(Pico/Cage HT)	Transitional forest	5	5	5	1
	Mature pine forest	4	4	4	1
	Immature pine forest	3	3	3	1
	Seedling-sapling stage	2	2	2	1
	Herbaceous stage	1	1	1	1

^a Meadow, steep slope, and riparian forest habitat types in this area have no clearly recognizable successional stages and are considered to remain constant through time.

Table 3-4. Age intervals for the six upland forest successional stages identified on the Little Firehole River Watershed under seven different rates of succession (cf Table 3-5).

COMMUNITY TYPE	Pico/Cage HT				Abla/Vasc HT		
	Typical stands	Early pine canopy mortality	Late pine canopy mortality	Slow restocking	Typical stands	Early pine canopy mortality	Late pine canopy mortality
1. Herbaceous stage	0-20	0-20	0-20	0-40	0-20	0-20	0-20
2. Seedling-sapling stage	20-40	20-40	20-40	40-80	20-40	20-40	20-40
3. Immature pine forest stage	40-150	40-150	40-150	80-200	40-150	40-150	40-150
4. Mature pine forest stage	150-200	150-170	150-300	200-250	150-300	150-180	150-350
5. Transitional stage	200-300	170-240	300-400	250-350	300-400	180-280	350-450
6. Climax forest stage	300+	240+	400+	350+	400+	280+	450+
Column in matrix SERE (Table 3-5)	1	2	3	4	5	6	7

Table 3-5. Seral stage endpoints in the matrix SERE used in the present study (cf Table 3-4).

	1	2	3	4	5	6	7
1	300	240	400	350	400	280	450
2	200	170	300	250	300	180	350
3	150	150	150	200	150	150	150
4	40	40	40	80	40	40	40
5	20	20	20	40	20	20	20

Table 3-6. Contents of the four data input files.

I. File No. 105--miscellaneous data

<u>LINE</u>	<u>FORMAT</u>	<u>DATA</u>
1	5I	ROWSIZE, COLSIZE, FIRSTYR, YRLIMIT, INCREMNT
2	F5.1	MAPYR
3	5F	PICOAREA, ABLAAREA, RIPFAREA, SLOPAREA, MEADAREA
4-8	7I	SERE(I,J) (row by row)
9	4(I4,X)	FIREYEAR(K)
10-19	11F	PATINDEX(I,J) (row by row)

II. File No. 106--stand age data for the matrix AGE

<u>LINE</u>	<u>FORMAT</u>	<u>DATA</u>
1-∞	3I	I,J,NUMBER

III. File No. 107--successional rate data for the matrix SEREINDX

<u>LINE</u>	<u>FORMAT</u>	<u>DATA</u>
1-∞	3I	I,J,INDX

IV. File No. 109--habitat-type data for the matrix VEGETYPE

<u>LINE</u>	<u>FORMAT</u>	<u>DATA</u>
1-∞	3I	I,J,TYPE

V. File No. 121--cells burned by the first simulated fire

<u>LINE</u>	<u>FORMAT</u>	<u>DATA</u>
1-∞	3I	I,J,ENDPT

VI. Files No. 122, 123, and 124--cells burned by second, third,
and fourth simulated fires, respectively (same composition
as File No. 121).

Table 3-7. Relative dissimilarity values in the matrix PATINDEX used in the present study.

			(Herbaceous stage)	(Seedling-sapling stage)	(Immature pine forest stage)	(Mature pine forest stage)	(Transitional stage)	(Climax Pico/Cage forest)	(Climax Abia/Vasc forest)	(Riparian forest)	(Steep slope forest)	(Meadow)
		1	2	3	4	5	6	7	8	9	10	11
(Herbaceous stage)	1	0	0	.5	.6	.7	.8	.9	.9	.9	.8	.8
(Seedling-sapling stage)	2	0	.5	0	.4	.6	.7	.8	.8	.8	.7	.9
(Immature pine forest stage)	3	0	.6	.4	0	.3	.4	.5	.5	.5	.4	1.0
(Mature pine forest stage)	4	0	.7	.6	.3	0	.4	.5	.5	.5	.3	1.0
(Transitional stage)	5	0	.8	.7	.4	.4	0	.3	.3	.3	.2	1.0
(Climax Pico/Cage forest)	6	0	.9	.8	.5	.5	.3	0	.3	.3	.2	1.0
(Climax Abia/Vasc forest)	7	0	.9	.8	.5	.5	.3	.3	0	.3	.2	1.0
(Riparian forest)	8	0	.9	.8	.5	.5	.3	.3	.3	0	.8	1.0
(Steep slope forest)	9	0	.8	.7	.4	.3	.2	.2	.2	.8	0	1.0
(Meadow)	10	0	.8	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0

Table 3-8. Landscape diversity indices (see main text).

I. Relative Richness (R)

$$R = \frac{T}{10} \times 100$$

where T = number of different
community-types
present (maximum
possible number is 10)

II. 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

H2(max) = maximum
possible value
of modified
Simpson's index

p_i = proportion of total
landscape area covered
by i^{th} community-type

T = number of different
community-types
present

III. Relative Patchiness (P)

$$P = \frac{\sum_{i=1}^N C_i}{\sum_{i=1}^N C_{max}} \times 100$$

where N = number of 5-ha cells
comprising the
landscape

C_i = contrast between
the i^{th} unit and
its adjacent
neighbor

C_{max} = maximum possible
contrast between
adjacent units

Table 3-9. Summary of program outputs for each year in which a landscape simulation is performed.

<u>LINE</u>	<u>DATA</u>
1	YEAR; no. of community-types present; relative richness; evenness; relative evenness; relative patchiness
2	Percent of landscape area occupied by each of 15 community-types (PERCENT(K)), printed sequentially from community-type 1 through community-type 15 (Table 3-3)
3	Percent of landscape area covered by early, middle, and late forest successional stages, respectively
4-53	(Optional) Map of community-types (Table 3-3) comprising the landscape (matrix STATE)

```

REAL MAPYR,PERCENT(15)
REAL EARLY,MIDDLE,LATE
REAL CELLNUMB,PER(10),PATCHSUM,PATINDEX(10,11),EVENNESS
REAL RICHNESS,PATCHNES,ECOUNTER
REAL EVENMAX,RELEVEN
REAL PICOAREA,ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA
INTEGER COMMUNITY(10),RCOUNTER,PATCHMAX
INTEGER AGE(50,49),SERE(5,7),SEREINDX(50,49)
INTEGER SUM(15),STATE(50,49),COMMTYPE(50,49)
INTEGER ROWSIZE,COLSIZE,YEAR,FIRSTYR,YRLIMIT,INCREMNT
INTEGER I,J,K,M,N,CELL(4),VEGETYPE(50,49)
INTEGER ENDPT,FIREYEAR(4),FILENUMB
INTEGER PICONUMB,ABLANUMB
C THE SUBROUTINE 'DATAFILL' INPUTS ALL REQUIRED PRELIMINARY
C DATA.
  CALL DATAFILL(ROWSIZE,COLSIZE,FIRSTYR,YRLIMIT,INCREMNT,
  MAPYR,SERE,FIREYEAR,PATINDEX,AGE,PICOAREA,ABLAAREA,
  RIPFAREA,SLOPAREA,MEADAREA,SEREINDX,VEGETYPE)
  M=1
  YEAR=FIRSTYR
C AFTER INITIALIZING THE FIRE COUNTER (M) AND THE YEAR,
C THE PROGRAM ENTERS A LOOP IN WHICH THE STATE OF EACH CELL
C IS DETERMINED AND LANDSCAPE DIVERSITY INDICES ARE COMPUTED
C FOR AN INCREMENTAL SERIES OF YEARS. THE LOOP TERMINATES
C AND THE PROGRAM ENDS AFTER THE SELECTED YEAR-LIMIT HAS
C BEEN REACHED.
  WHILE(YEAR.LE.YRLIMIT)DO
C THE FOLLOWING IF/THEN STATEMENT DETERMINES WHETHER THE YEAR
C CURRENTLY BEING ANALYZED IS A FIRE YEAR. IF SO, APPROPRIATE
C CELLS IN THE MATRIX 'AGE' ARE RETURNED TO AGE 0.
    IF((M.LT.5).AND.(YEAR.GE.FIREYEAR(M)))THEN
      FILENUMB=120+M
100      READ(FILENUMB,110,END=130)I,J,ENDPT
110      FORMAT(3I)
      AGE(I,J)=YEAR-FIREYEAR(M)
      DO 120 N=J,ENDPT,1
        AGE(I,N)=AGE(I,J)
120      CONTINUE
      GOTO 100
130      M=M+1
      ENDIF
      DO 140 K=1,10,1
        COMMUNITY(K)=0
140      CONTINUE
      DO 150 K=1,15,1
        SUM(K)=0
150      CONTINUE
      PATCHSUM=0.0
      PATCHMAX=0
C AFTER INITIALIZING THE LANDSCAPE DIVERSITY INDEX COUNTERS.

```

C THE FOLLOWING GROUP OF DECISION STATEMENTS CLASSIFIES EACH
 C CELL AS ONE OF 10 DIFFERENT COMMUNITY-TYPES.

```

DO 170 J=1, COLSIZE, 1
  DO 160 I=1, ROWSIZE, 1
    IF (AGE(I,J).GE.0) THEN
      IF (VEGETYPE(I,J).EQ.5) THEN
        STATE(I,J)=10
        COMMTYPE(I,J)=10
        COMMUNITY(10)=1
      ELSEIF (VEGETYPE(I,J).EQ.4) THEN
        STATE(I,J)=9
        COMMTYPE(I,J)=9
        COMMUNITY(9)=1
      ELSEIF (VEGETYPE(I,J).EQ.3) THEN
        STATE(I,J)=8
        COMMTYPE(I,J)=8
        COMMUNITY(8)=1
      ELSE
        IF (AGE(I,J).GT.SERE(1,SEREINDX(I,J))) THEN
          IF (VEGETYPE(I,J).EQ.2) THEN
            STATE(I,J)=7
            COMMTYPE(I,J)=7
            COMMUNITY(7)=1
          ELSE
            STATE(I,J)=6
            COMMTYPE(I,J)=6
            COMMUNITY(6)=1
          ENDIF
        ELSEIF (AGE(I,J).GT.SERE(2,SEREINDX(I,J))) THEN
          IF (VEGETYPE(I,J).EQ.2) THEN
            STATE(I,J)=15
          ELSE
            STATE(I,J)=5
          ENDIF
          COMMTYPE(I,J)=5
          COMMUNITY(5)=1
        ELSEIF (AGE(I,J).GT.SERE(3,SEREINDX(I,J))) THEN
          IF (VEGETYPE(I,J).EQ.2) THEN
            STATE(I,J)=14
          ELSE
            STATE(I,J)=4
          ENDIF
          COMMTYPE(I,J)=4
          COMMUNITY(4)=1
        ELSEIF (AGE(I,J).GT.SERE(4,SEREINDX(I,J))) THEN
          IF (VEGETYPE(I,J).EQ.2) THEN
            STATE(I,J)=13
          ELSE
            STATE(I,J)=3
          ENDIF
        ENDIF
      ENDIF
    ENDIF
  ENDIF
END DO

```

```

      COMMTYPE(I,J)=3
      COMMUNITY(3)=1
    ELSEIF (AGE(I,J).GT.SERE(5,SEREINDX(I,J))) THEN
      IF (VEGETYPE(I,J).EQ.2) THEN
        STATE(I,J)=12
      ELSE
        STATE(I,J)=2
      ENDIF
      COMMTYPE(I,J)=2
      COMMUNITY(2)=1
    ELSE
      IF (VEGETYPE(I,J).EQ.2) THEN
        STATE(I,J)=11
      ELSE
        STATE(I,J)=1
      ENDIF
      COMMTYPE(I,J)=1
      COMMUNITY(1)=1
    ENDIF
    AGE(I,J)=AGE(I,J)+INCREMNT
  ENDIF
  SUM(STATE(I,J))=SUM(STATE(I,J))+1
  CELL(1)=COMMTYPE(I-1,J)
  CELL(2)=COMMTYPE(I,J-1)
  CELL(3)=CELL(1)+1
  CELL(4)=CELL(2)+1
  PATCHSUM=PATCHSUM+PATINDEX(COMMTYPE(I,J),
    CELL(3))+PATINDEX(COMMTYPE(I,J),CELL(4))
  IF ((CELL(1).GT.0).AND.(CELL(2).GT.0)) THEN
    PATCHMAX=PATCHMAX+2
  ELSE
    IF ((CELL(1).GT.0).OR.(CELL(2).GT.0)) THEN
      PATCHMAX=PATCHMAX+1
    ENDIF
  ENDIF
  ELSE
    STATE(I,J)=0
    COMMTYPE(I,J)=0
  ENDIF
160      CONTINUE
170      CONTINUE
C THE SUBROUTINE 'INDICES' COMPUTES ALL LANDSCAPE
C DIVERSITY INDICES.
      CALL INDICES(RICHNESS,EVENNESS,PATCHNES,PERCENT,
        $ COMMUNITY,SUM,PATCHSUM,PATCHMAX,RCOUNTER,RELEVEN,
        $ EARLY,MIDDLE,LATE,PICOAREA,ABLAAREA,
        $ RIPFAREA,SLOPAREA,MEADAREA)
C LANDSCAPE DIVERSITY INDICES ARE PRINTED, THEN AN
C INCREMENT IS ADDED TO THE YEAR AND THE PROCESS IS REPEATED.
      PRINT 180,YEAR,RCOUNTER,RICHNESS,EVENNESS,RELEVEN,PATCHNES

```



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180      FORMAT(X,'YEAR:',I4,3X,'NO. COMM.-TYPES=',I2,X,
$        '(RICHNESS=',F5.1,')',3X,'EVENNESS=',F6.3,X,
$        '(REL. EVENNESS=',F5.1,')',3X,'PATCHINESS=',F5.1)
      PRINT 190,(PERCENT(K),K=1,15)
190      FORMAT(3X,'PERCENT(1-15):',X,15(F5.2,X))
      PRINT 200,EARLY,MIDDLE,LATE
200      FORMAT(3X,'EARLY STAGES=',F5.2,3X,'MIDDLE STAGES=',F5.2,
$        3X,'LATE STAGES=',F5.2)
      IF(((YEAR-FIRSTYR)/MAPYR).EQ.(INT((YEAR-FIRSTYR)/MAPYR))) THEN
        DO 220 I=1,ROWSIZE
          PRINT 210,COLSIZE,(STATE(I,J),J=1,COLSIZE)
210          FORMAT(N(I2))
220          CONTINUE
        ENDIF
        YEAR=YEAR+INCREMNT
      ENDWHILE
      STOP
      END
      SUBROUTINE DATAFILL(ROWSIZE,COLSIZE,FIRSTYR,YRLIMIT,
$INCREMNT,MAPYR,SERE,FIREYEAR,PATINDEX,AGE,
$PICOAREA,ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA,
$SEREINDX,VEGETYPE)
      REAL PICOAREA,ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA
      REAL MAPYR,PATINDEX(10,11)
      INTEGER ROWSIZE,COLSIZE,FIRSTYR,YRLIMIT,INCREMNT
      INTEGER SERE(5,7),FIREYEAR(4),AGE(50,49),SEREINDX(50,49)
      INTEGER VEGETYPE(50,49),I,J,NUMBER,INDX,TYPE
      READ(105,300)ROWSIZE,COLSIZE,FIRSTYR,YRLIMIT,INCREMNT
300      FORMAT(5I)
      READ(105,310)MAPYR
310      FORMAT(F5.1)
      READ(105,320)PICOAREA,ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA
320      FORMAT(5F)
      READ(105,340)((SERE(I,J),J=1,7),I=1,5)
340      FORMAT(7I)
      READ(105,350)(FIREYEAR(K),K=1,4)
350      FORMAT(4(I4,X))
      READ(105,360)((PATINDEX(I,J),J=1,11),I=1,10)
360      FORMAT(11F)
      DO 380 I=1,ROWSIZE,1
        DO 370 J=1,COLSIZE,1
          AGE(I,J)=0
          SEREINDX(I,J)=0
          VEGETYPE(I,J)=0
370          CONTINUE
380          CONTINUE
390      READ(106,400,END=410) I,J,NUMBER
400      FORMAT(3I)
          AGE(I,J)=NUMBER
          GOTO 390

```

```

410  CONTINUE
420  READ(107,400,END=430) I,J,INDX
      SEREINDX(I,J)=INDX
      GOTO 420
430  CONTINUE
440  READ(109,400,END=450) I,J,TYPE
      VEGETYPE(I,J)=TYPE
      GOTO 440
450  CONTINUE
      DO 470 I=1,ROWSIZE,1
        DO 460 J=1,COLSIZE,1
          IF (AGE(I,J).EQ.0) THEN
            AGE(I,J)=AGE(I,J-1)
          ENDIF
          IF (SEREINDX(I,J).EQ.0) THEN
            SEREINDX(I,J)=SEREINDX(I,J-1)
          ENDIF
          IF (VEGETYPE(I,J).EQ.0) THEN
            VEGETYPE(I,J)=VEGETYPE(I,J-1)
          ENDIF
        DO 460 J=1,COLSIZE,1
      DO 470 I=1,ROWSIZE,1
460  CONTINUE
470  CONTINUE
      RETURN
      END
      SUBROUTINE INDICES(RICHNESS,EVENNESS,PATCHNES,PERCENT,
$COMMUNITY,SUM,PATCHSUM,PATCHMAX,RCOUNTER,RELEVEN,
$EARLY,MIDDLE,LATE,PICOAREA,ABLAAREA,
$RIPFAREA,SLOPAREA,MEADAREA)
      REAL RICHNESS,EVENNESS,PATCHNES,PATCHSUM,PERCENT(15)
      REAL EARLY,MIDDLE,LATE,DIVERSTY
      REAL CELLNUMB,PER(10),ECOUNTER,RELEVEN
      REAL EVENMAX,PICOAREA
      REAL ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA
      INTEGER PICONUMB,ABLANUMB
      INTEGER COMMUNITY(10),SUM(15),PATCHMAX,K,RCOUNTER
      RCOUNTER=0
      DO 500 K=1,10,1
        RCOUNTER=RCOUNTER+COMMUNITY(K)
500  CONTINUE
      RICHNESS=RCOUNTER/10.0*100
      CELLNUMB=0.0
      DO 510 K=1,15,1
        CELLNUMB=CELLNUMB+SUM(K)
510  CONTINUE
      DO 520 K=1,15,1
        PERCENT(K)=SUM(K)/CELLNUMB*100.0
520  CONTINUE
      EARLY=PERCENT(1)+PERCENT(2)+PERCENT(11)+PERCENT(12)
      MIDDLE=PERCENT(3)+PERCENT(4)+PERCENT(13)+PERCENT(14)
      LATE=PERCENT(5)+PERCENT(6)+PERCENT(7)+PERCENT(15)

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PER(1)=(SUM(1)+SUM(11))/CELLNUMB
PER(2)=(SUM(2)+SUM(12))/CELLNUMB
PER(3)=(SUM(3)+SUM(13))/CELLNUMB
PER(4)=(SUM(4)+SUM(14))/CELLNUMB
PER(5)=(SUM(5)+SUM(15))/CELLNUMB
DO 530 K=6,10,1
    PER(K)=SUM(K)/CELLNUMB
530  CONTINUE
    ECOUNTER=0.0
    DO 540 K=1,10,1
        ECOUNTER=ECOUNTER+PER(K)**2
540  CONTINUE
    EVENNESS=-LOG(ECOUNTER)
C   THE SUBROUTINE 'MAXEVEN' COMPUTES THE MAXIMUM POSSIBLE
C   EVENNESS VALUE FOR THE NUMBER OF COMMUNITY-TYPES PRESENT
C   ('EVENMAX').
    CALL MAXEVEN(EVENMAX,SUM,PICOAREA,ABLAAREA,
$RIPFAREA,SLOPAREA,MEADAREA)
    RELEVEN=EVENNESS/EVENMAX*100
    PATCHNES=PATCHSUM/PATCHMAX*100
    DIVERSITY=(RICHNESS+RELEVEN+PATCHNES)/3
    RETURN
    END
    SUBROUTINE MAXEVEN(EVENMAX,SUM,PICOAREA,ABLAAREA,
$RIPFAREA,SLOPAREA,MEADAREA)
    REAL EVENMAX,PICOAREA,ABLAAREA,RIPFAREA,SLOPAREA,MEADAREA
    INTEGER SUM(15),PICONUMB,ABLANUMB,K
    PICONUMB=0
    DO 600 K=1,6,1
        IF(SUM(K).GT.0) THEN
            PICONUMB=PICONUMB+1
        ENDIF
600  CONTINUE
    ABLANUMB=0
    DO 610 K=11,15,1
        IF(SUM(K).GT.0) THEN
            ABLANUMB=ABLANUMB+1
        ENDIF
610  CONTINUE
    IF(SUM(7).GT.0) THEN
        ABLANUMB=ABLANUMB+1
    ENDIF
    EVENMAX=-LOG(((PICOAREA/PICONUMB)**2)*PICONUMB+
$(ABLAAREA/ABLANUMB)**2)*ABLANUMB+
$RIPFAREA**2+SLOPAREA**2+MEADAREA**2)
    RETURN
    END

```

APPENDIX 4

CLUSTER ANALYSIS AND CLASSIFICATION
OF
SUBALPINE FOREST SUCCESSIONAL STAGES
IN
YELLOWSTONE NATIONAL PARK

Despain (1977) described six successional stages in the subalpine forests of Yellowstone National Park (Table 4-1). Stage 0 includes recently disturbed sites where lodgepole pine is becoming re-established, the trees being < 2m tall. Stage 1 is characterized by canopy closure and maturation of the even-aged lodgepole pine cohort. During stage 2, subalpine fir, Engelmann spruce, and whitebark pine (all < 1m tall) become established beneath the mature pine canopy on mesic sites, with little or no understory on dry sites. Stage 3 is marked by extensive mortality in the even-aged pine canopy with replacement by fir, spruce, whitebark pine, and/or a second generation of lodgepole pine (specific species composition being determined by site characteristics). In stage 4 the initial, even-aged cohort of lodgepole pine has almost completely disappeared from the canopy, having been replaced by an all-aged stand of fir, spruce, whitebark pine, and/or second-generation lodgepole pine. In the fifth stage, all of the trees that become established during stages 1 - 2 have been replaced by individuals germinating during later stages. Stages 4 - 5 are considered climax.

My observations on the Little Firehole River Watershed generally supported Despain's (1977) classification, although I found it useful to subdivide his earliest successional stage into two stages, differing in structure, and to disregard his fifth stage, which is difficult to distinguish from the preceding stage. Thus, I treated the six forest successional stages listed in Tables 1 and 4-1 and described in the section on Study Area in the main text.

Table 4-1. Forest successional stages recognized by Despain (1977) and the corresponding community-types treated in the present study. Descriptions apply to the taxa in the present study (see section on Study Area in main text).

SUCCESSIONAL STAGE (Despain 1977)	COMMUNITY TYPE (Present study)	DESCRIPTION
0	1	Herbaceous stage
0	2	Seedling-sapling stage
1	3	Immature pine forest
2	4	Mature pine forest
3	5	Transitional stage
4	6 or 7 ^a	Climax forest
5	6 or 7 ^a	Climax forest

^aCommunity-type 6 is the climax stage in the Pico/Cage HT; community-type 7 is the climax stage in the Abia/Vasc HT.

To test the validity of these two subjective classifications (Table 4-1) I collected quantitative forest structure data in 18 upland stands along a chronosequence on the Little Firehole River Watershed and performed a cluster analysis using Euclidean distance (square root of the sum of squares of differences between stands) as a measure of dissimilarity (Dixon 1977). The cluster analysis was based on four stand characteristics: relative density and basal area of climax species (i.e., subalpine fir, Engelmann spruce, whitebark pine, and/or second-generation lodgepole pine, depending on site); percent tree mortality in the even-aged lodgepole pine canopy; and amount of dead, fallen, woody material > 2.5cm diameter. Living and dead standing stems were tallied by species and dbh class in one or two circular plots subjectively located in a representative portion of the stand. Plot size ranged from 0.03 - 0.14 ha, with the smaller plots in dense stands. Fallen trees that had been rooted within the plot also were tallied and classed as sound or rotten (i.e., in early stages of decomposition). Second-generation lodgepole pine usually could be distinguished from the pioneer cohort on the basis of size and crown shape. To determine percent mortality in the even-aged pine canopy I first estimated what the tree density had been when the even-aged pine cohort first reached maturity (usually around stand age 150 yr in this area), based on the total number of dominant pine in the plot(s), including both living and dead, standing and fallen stems. I then divided this number into the number of dead pine (former dominants) in the plot(s),

multiplying by 100 to arrive at percent mortality. Former dominants could be recognized among standing and fallen dead trees on the basis of size and degree of decomposition. Total dead, fallen, woody material was sampled with the planar intercept method (Brown 1974).

Fig. 4-1 shows the dendrogram resulting from the cluster analysis. The number of distinct groups defined by this method depends on the level of dissimilarity considered significant; at Euclidean distance 1.00 there are seven clusters corresponding fairly closely to the subjective classifications shown in Tables 1 and 4-1. The earliest post-fire successional stage recognized in this study (herbaceous stage; community-type 1 (CT 1) in Table 4-1) currently cannot be found on the Little Firehole River Watershed, and is not shown in Fig. 4-1. The second successional stage (CT 2) is represented by a 29-yr-old stand that forms cluster 3 in Fig. 4-1. Four stands in the third successional stage (CT 3), ranging from 73-122 yr old, are grouped in cluster 1 together with two stands (144 and 183 yr old) in the fourth stage (CT 4). Cluster 2 is composed of three additional stands in the fourth stage, ranging from 183 - 239 yr old. Although the third and fourth successional stages are not completely separated in the cluster analysis, I felt justified in treating them as distinct community-types because they usually can be distinguished easily in the field on the basis of tree height and the distance between the ground and the lowermost branches (characteristics that were not treated in the cluster analysis).

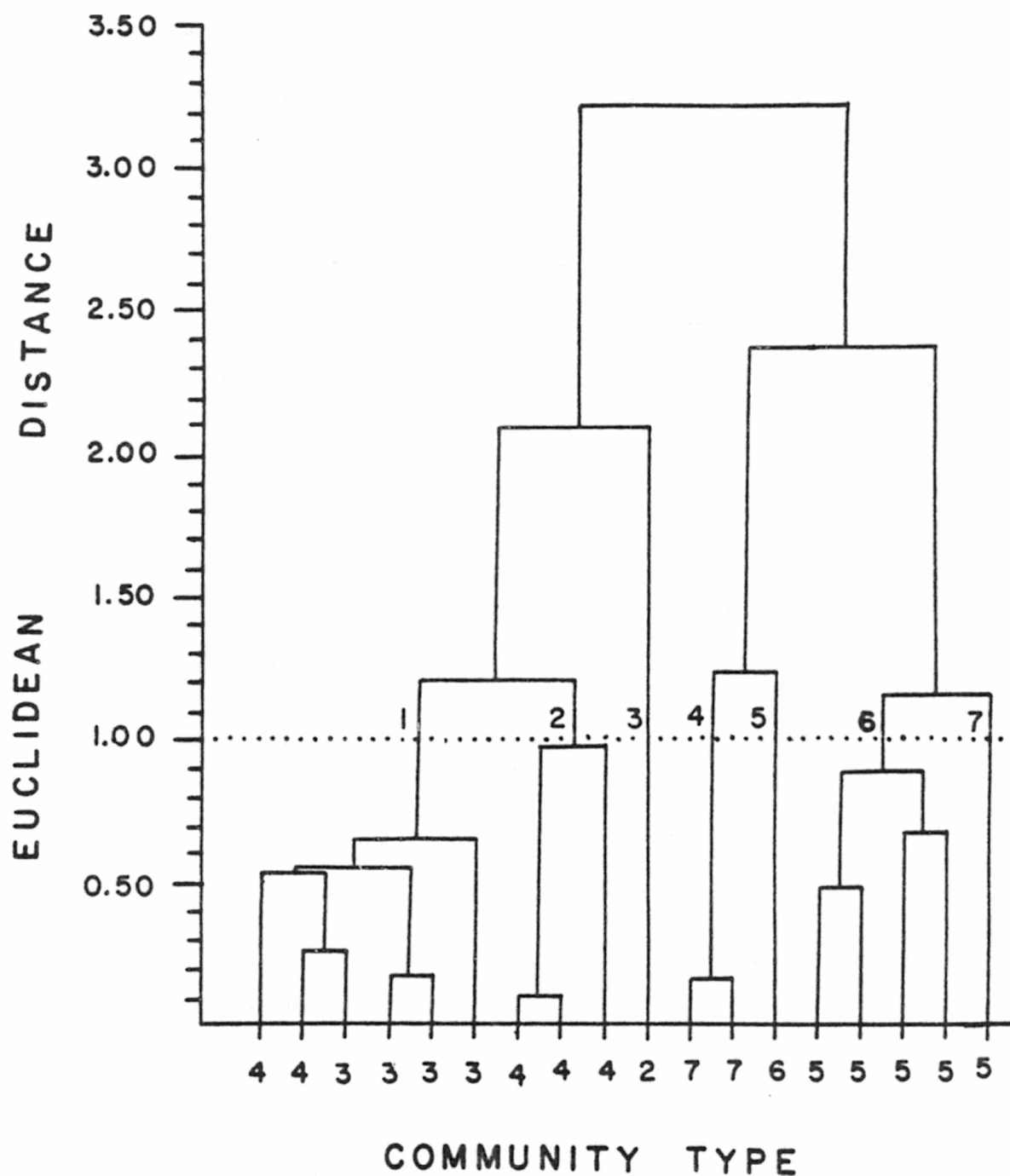


Figure 4-1. Dendrogram produced by cluster analysis of 18 upland stands showing seven distinct groups using Euclidean distance 1.00 as the level of differentiation. Euclidean distance is the square root of the sum of squares of differences between stands (see text). Community-types are defined in Table 1 (main text) and described in the section on Study Area.

The fifth successional stage (CT 5) is represented by the four stands in cluster 6, ranging from 239 - 350 yr old, plus a 450-yr-old stand comprising cluster 7. This latter stand actually appears transitional between the fifth and sixth stages. The sixth (climax) stage in the Pico/Cage HT (CT 6) is represented by a 400+-yr-old stand forming cluster 5, with the climax stage in the Abia/Vasc HT (CT 7) being represented by the two stands in cluster 4, 450+ and 550+-yr-old.

REFERENCES CITED

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- Dixon, W. J. (editor). 1977. BMD Biomedical Computer Programs. University of California Press.

